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"THE FORM AND STRUCTURE OF THE HUMAN CLAUSTRUM".

by

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INTRODUCTION.

The sheet of grey matter lying between the insular cortex and putamen is said to have been first described (as the nucleus taeniaformis) by Vicq d'Azyr. The name "claustrum" was introduced by Burdach.

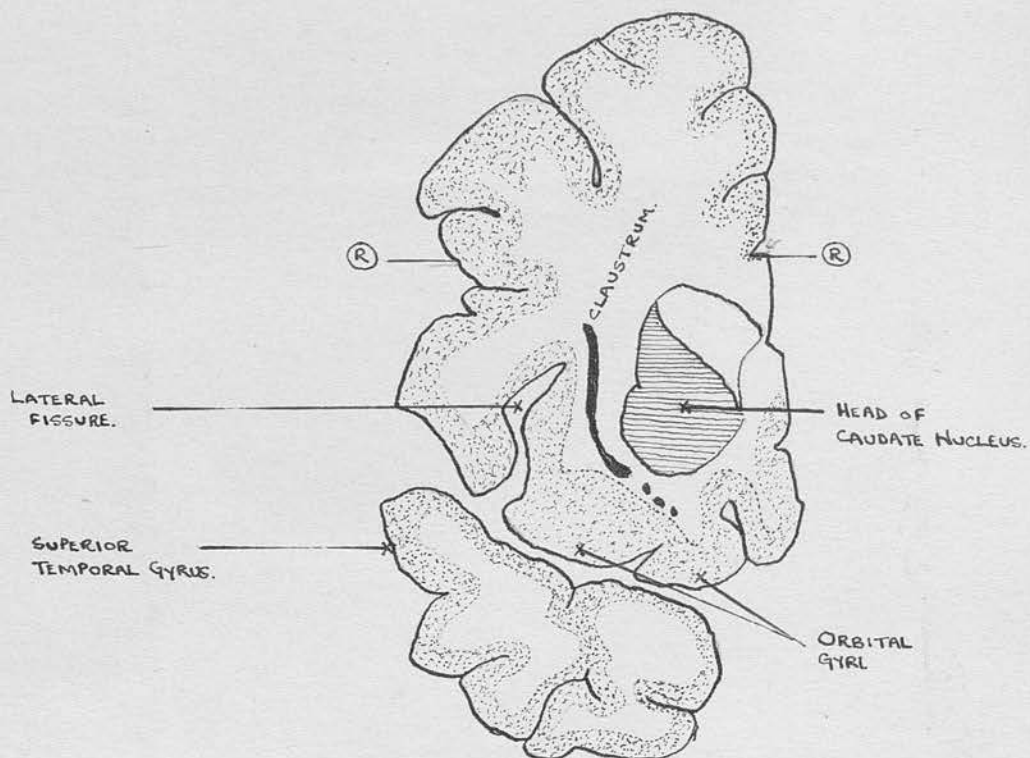
The claustrum was early assumed to constitute the deepest layer of the insular cortex. This view was accepted by many authors and is still quoted in some current text-books. The inadequacy of the evidence upon which it was based has been demonstrated by several anatomists, especially by Professor Ebers Landau of Lausanne, who devoted an important series of papers to the matter. It is therefore necessary to investigate the claustrum as a formation sui generis. The facts at present available suggest that the claustrum is no mere dependancy or stratum of the insular cortex, and that it is connected to many regions of the brain. Its function is quite unknown.

Relatively little study has been given to the claustrum itself; many relevant facts are scattered in publications primarily concerned with other matters; ontogenetic and phylogenetic researches have, so far, tended to confuse rather than to clarify the subject.

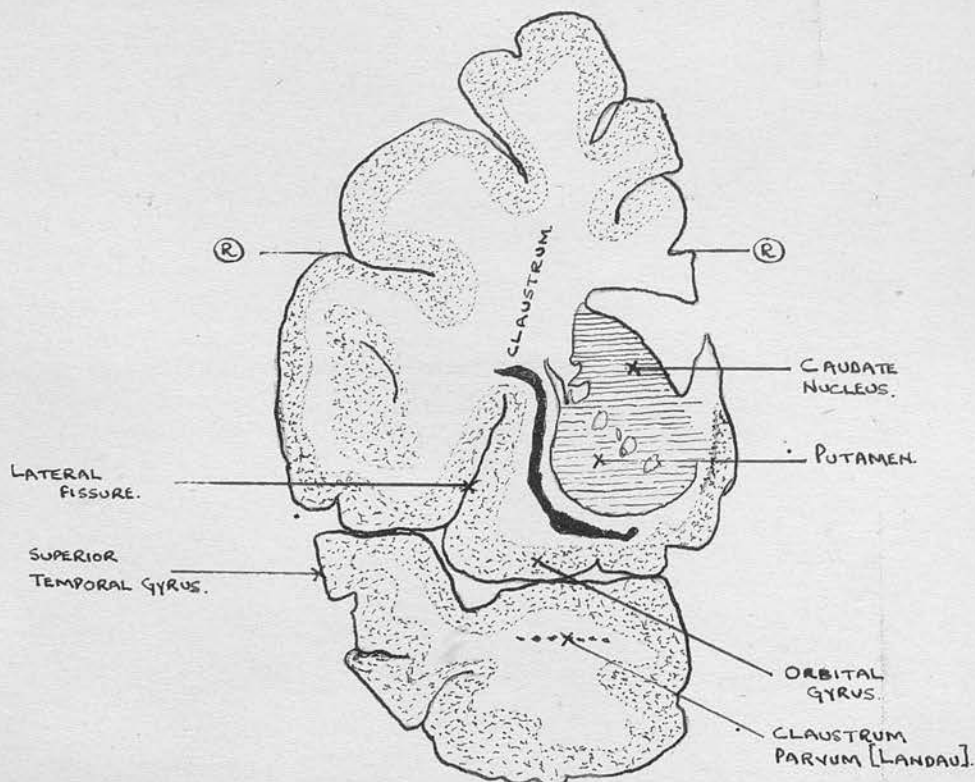
The present work is restricted to the investigation of the macroscopic form and histological characteristics of the adult human claustrum, to a discussion of the literature dealing with these topics, and to an attempt to synthesize the information thus obtained.

MACROSCOPIC ANATOMY OF THE CLAUSTRUM.

SECTION 11.



SECTION 12.



MATERIALS AND METHODS.

A grossly normal right hemisphere was cut in a macrotome in the frontal-vertical plane. The slices (5 m.m. thick) were numbered in serial order (proceeding antero-posteriorly) and were impregnated by the method of Brown (1939). Tracings were prepared from these sections, and the accompanying diagrams drawn therefrom. Additional information was obtained from examination of the independant series of slices (three hemispheres) from which the histological material was obtained. The diagrams were orientated about an arbitrary reference line marked (R) approximately parallel to the long axis of the trunk of the corpus callosum. Details are given in the Appendix on technical Methods.

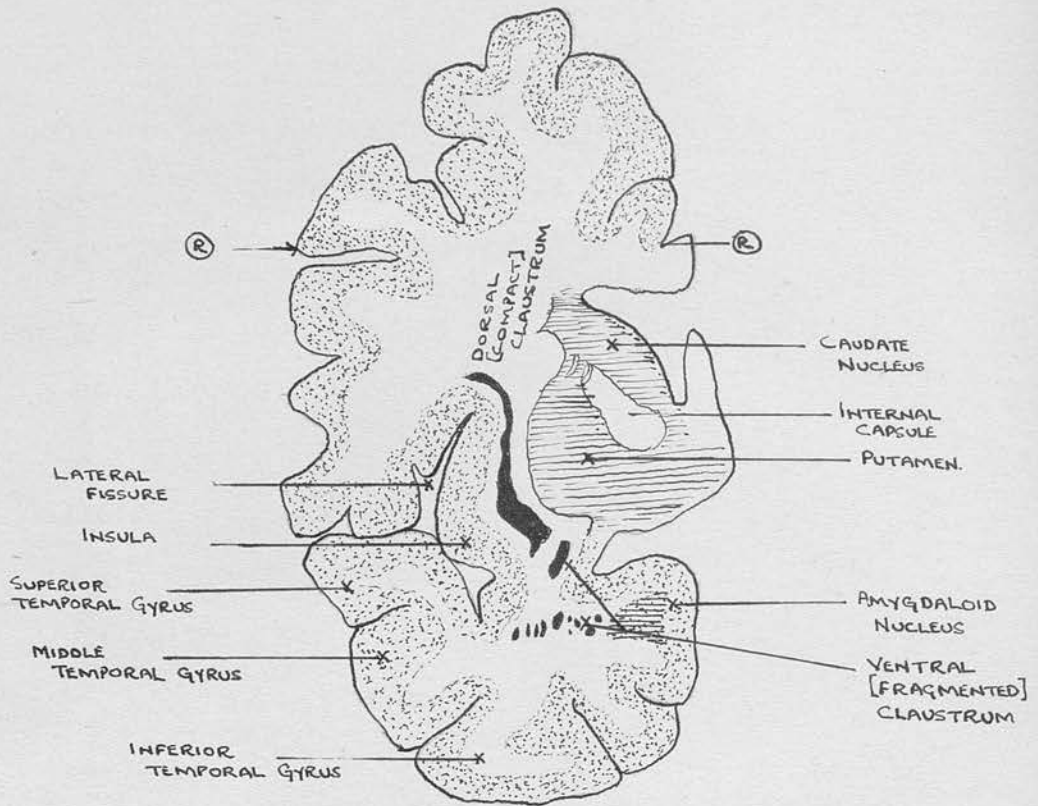
PERSONAL OBSERVATIONS.

The macroscopic sections will be described in serial order.

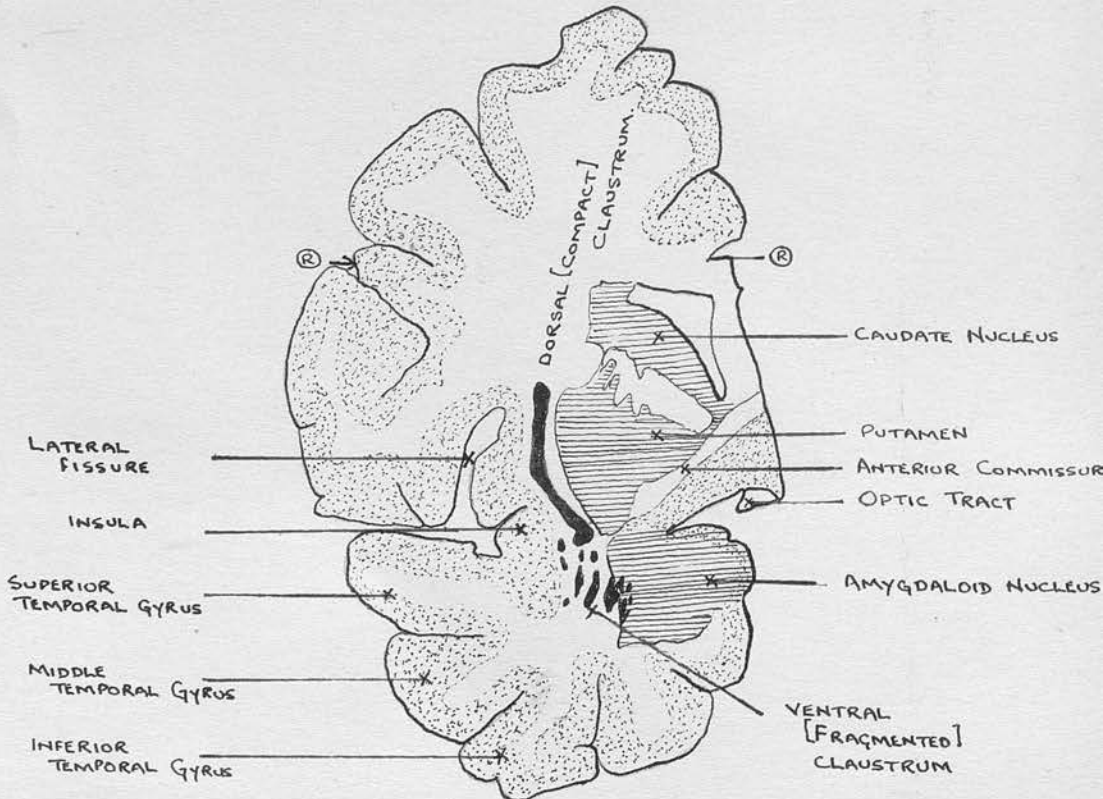
Section 11. (50 m.m. posterior to the frontal pole).

The claustrum first appears in this section. It is a thin medially concave streak of grey matter lying between insula and striatum. The apex of the claustrum extends slightly above the level of the circular sulcus of the insula, and follows the curve of the insular cortex; the middle portion roughly corresponds to the lateral border of the striatum. The lower part of the claustrum, which is discontinuous, passes ventro-medially into the sub-lenticular white matter. Both capsules are broad, the external being the wider. The temporal

SECTION 13.



SECTION 14.



lobe shows no features of interest.

Section 12.

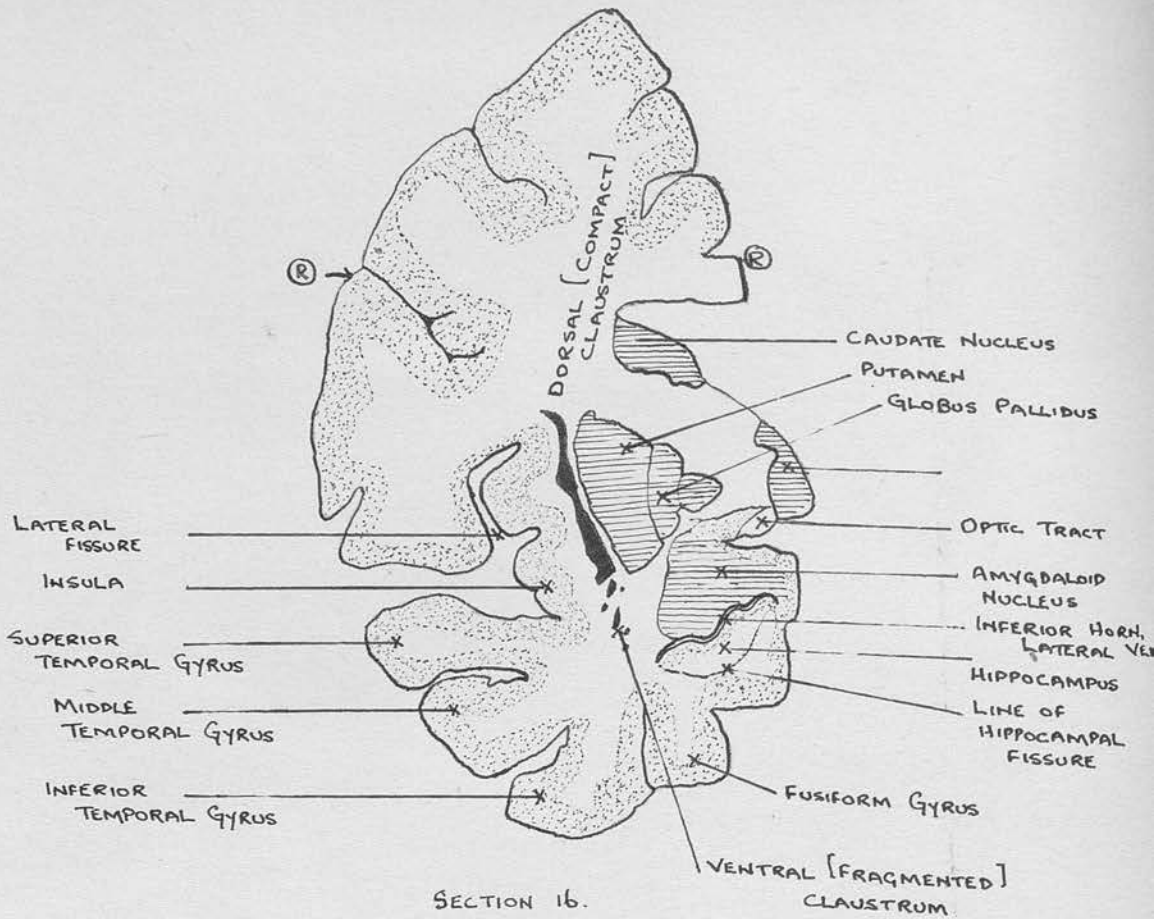
The claustrum forms a sinuous curve, slightly thinned at the junction of the middle and inferior thirds. The apex of the claustrum lies close to the insular cortex and is directed laterally; the remainder of the claustrum follows the outline of the lateral and ventral margins of the putamen. The inferior part of the claustrum lies dorsal to the cortex of the orbital gyri, but does not appear to fuse with it. The extreme capsule is the wider throughout most of its extent.

The superior portion of the white matter of the temporal lobe contains a slender line of small grey points. These lie transversely about $\frac{1}{4}$ m.m. below, and parallel to, the cortex of the superior surface of the temporal lobe. This horizontal streak closely approaches the temporal cortex at its lateral and medial ends but is not continuous with it. This formation is the "Claustrum Parvum", so named by Landau, who described it in 1936.

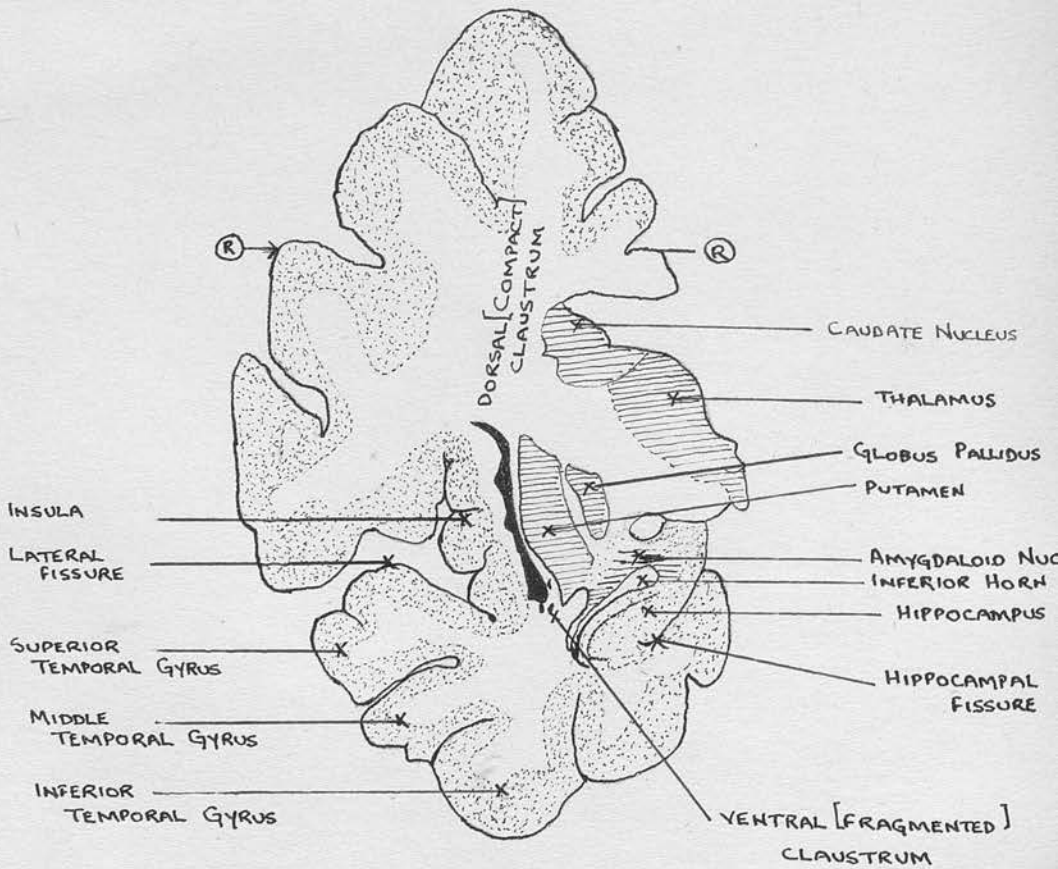
Section 13.

The claustrum is sinuous in outline. The upper part is close to the insular cortex and follows its contour. The apex bends over the circular sulcus and extends laterally for about 2 m.m. The remainder of the claustrum is thicker and tends to follow the lateral border of the putamen. Close to the inferior end of the claustrum there is an isolated mass of grey matter

SECTION 15.



SECTION 16.



adjacent to the basal cortex, but apparently independent of it. An irregular cluster of small grey islets extends horizontally across the white matter at the level of the lower margin of the insula. This cluster occupies the same level as that in which the claustrum parvum was found in Section 12. The external capsule is the wider.

Section 14.

The claustrum forms a thick bar, slightly concave medially, which follows the lateral border of the putamen, and which extends from the upper margin of the insula to the lower (infero-lateral) border of the putamen. Although in this section the insular gyri and sulci are well-developed, the lateral edge of the claustrum shows no corresponding irregularities.

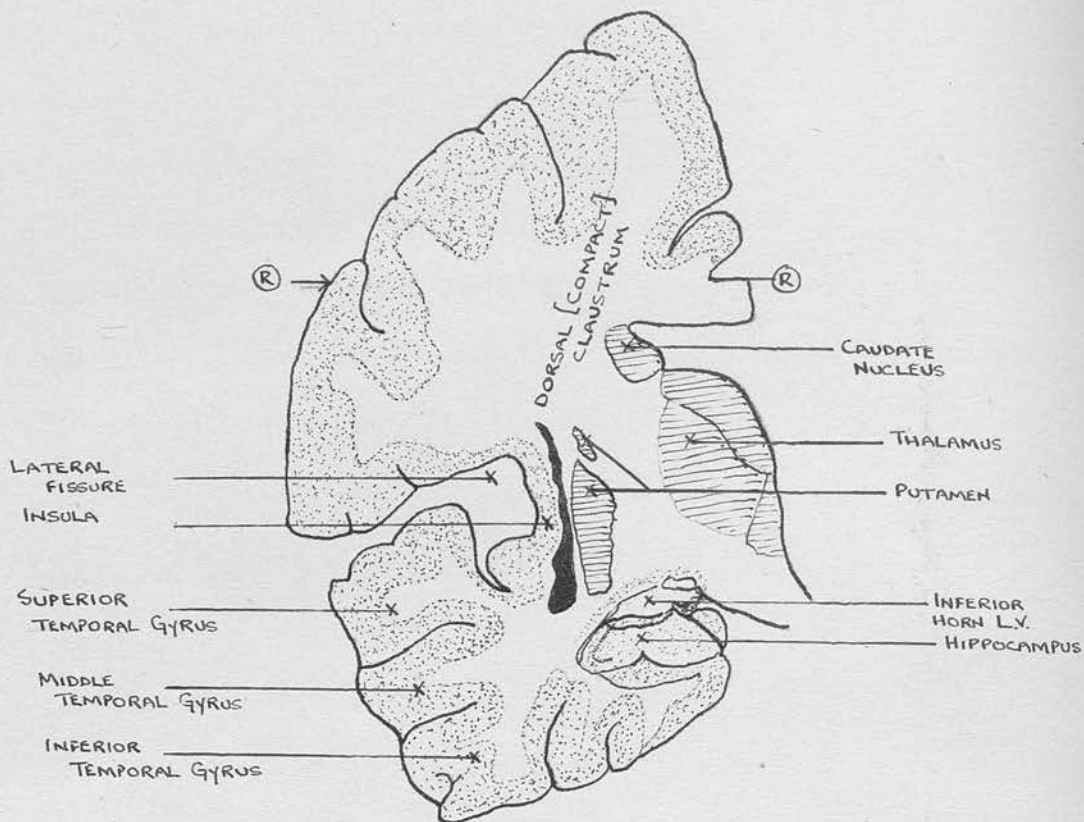
The anterior commissure is clearly seen, passing ventro-laterally towards the inferior part of the putamen. It is not macroscopically continuous with the external capsule.

Irregular islets of grey matter (mainly elliptical with a vertical major axis) are scattered in the area between the lower part of the insular cortex and the lateral border of the amygdaloid complex. The external capsule is the wider.

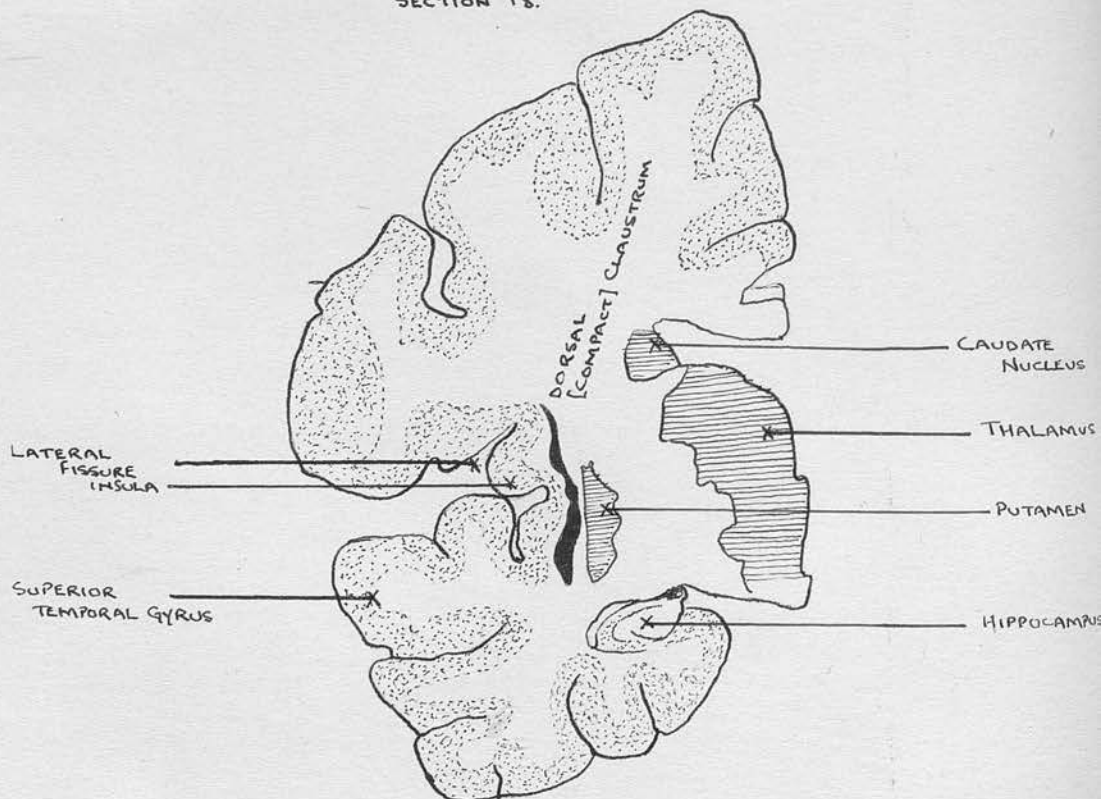
Section 15.

The claustrum is slender, tapering to an apex which is directed supero-laterally. The lateral border of the claustrum is irregular, and these irregularities

SECTION 17.



SECTION 18.



approximately correspond to the outline of the insular cortex. The medial border of the claustrum is smooth, so that the thickness of the claustrum varies according to the undulations of its lateral edge. The lower end of the claustrum is at the level of the infero-lateral border of the putamen. A few very small grey islets are situated between the lower portion of the cortex of the insula and the lateral border of the amygdaloid complex. The extreme capsule is much wider than the external capsule, which is very narrow inferiorly.

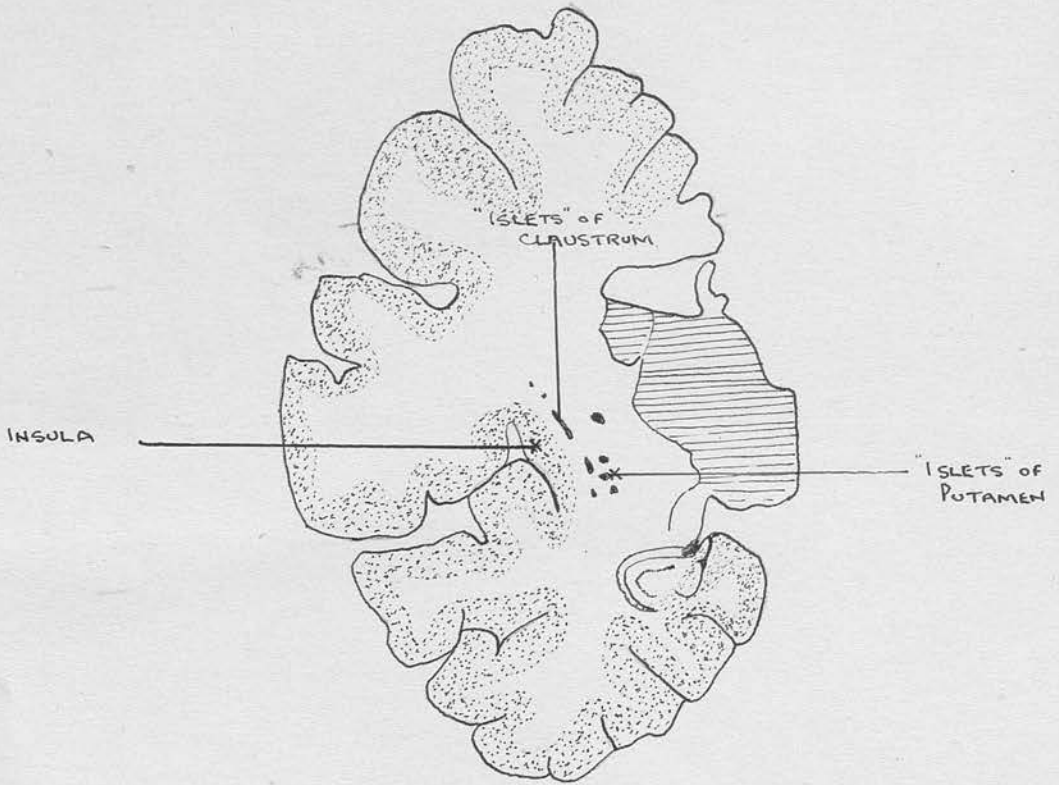
Section 16.

The claustrum is slender. The apex extends supero-laterally and ends at the level of the superior margin of the insula. The lateral border is irregular, the irregularities roughly corresponding to those of the insular cortex. The inferior part of the claustrum is thicker and terminates opposite the infero-lateral border of the putamen. A few isolated points of grey matter adjoin its inferior extremity. The extreme capsule is the wider.

Section 17.

The claustrum forms a vertical bar, broader inferiorly. which extends from the superior to the inferior margins of the insula. Its lateral border closely follows the outline of the insular cortex. The lower two-thirds of its medial border is parallel to the outline of the putamen. Both capsules are thin and are approximately equal in width. There are no isolated grey masses.

SECTION 19.



Section 18.

The claustrum is a sinuous streak of varying thickness, extending from the upper to the lower margins of the insula. Its form approximately corresponds to the sulci and gyri of the insula. The external capsule is less extensive vertically than the extreme capsule. There are no isolated grey masses.

Section 19.

The claustrum is represented by small isolated masses of grey matter, arranged in linear order and lying medial to another group of grey islets representing the putamen. The claustrum is not visible in more posterior sections.

In order to obtain a general view of the form of the claustrum a series of tracings of the claustral outline was made from the sections described above. The individual outlines are arbitrarily spaced $\frac{3}{4}$ inch apart, and are correctly orientated (as regards vertical distance) from the reference line (R) Fig.2. The drawings show that the claustrum gradually changes in shape when followed antero-posteriorly. In the anterior sections it is S-shaped, then concave medially, then assumes a flattened shape, elongated vertically, and finally becomes concave laterally. The formation as a whole descends in the middle group of sections, gradually rising again in the posterior sections. The apex is usually directed supero-laterally, and the base is frequently thickened. The isolated grey masses occupy a relatively constant level with respect to the reference plane (R). It should be noted that no isolated grey

FIGURE 1.

LATERAL VIEW OF CLAUSTRUM ON PROFILE OF
CEREBRAL HEMISPHERE.

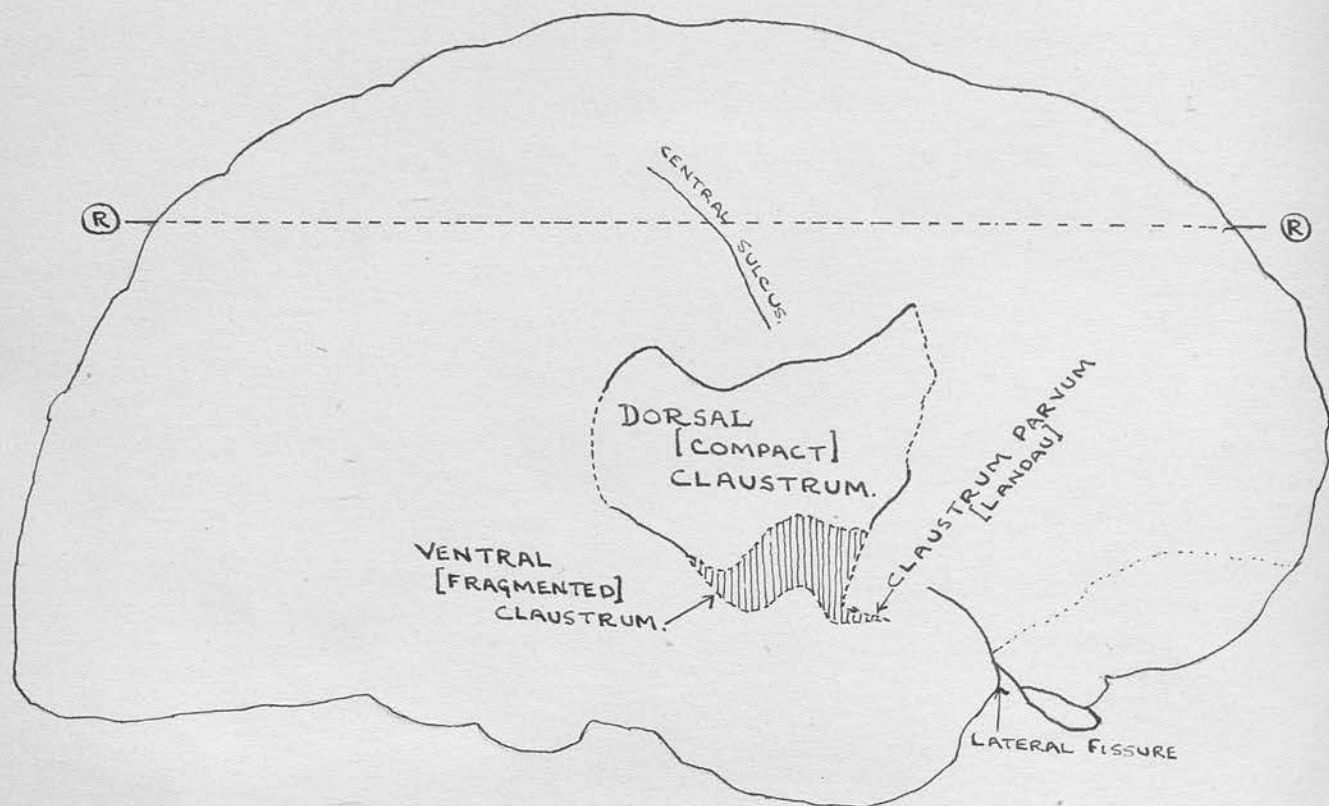
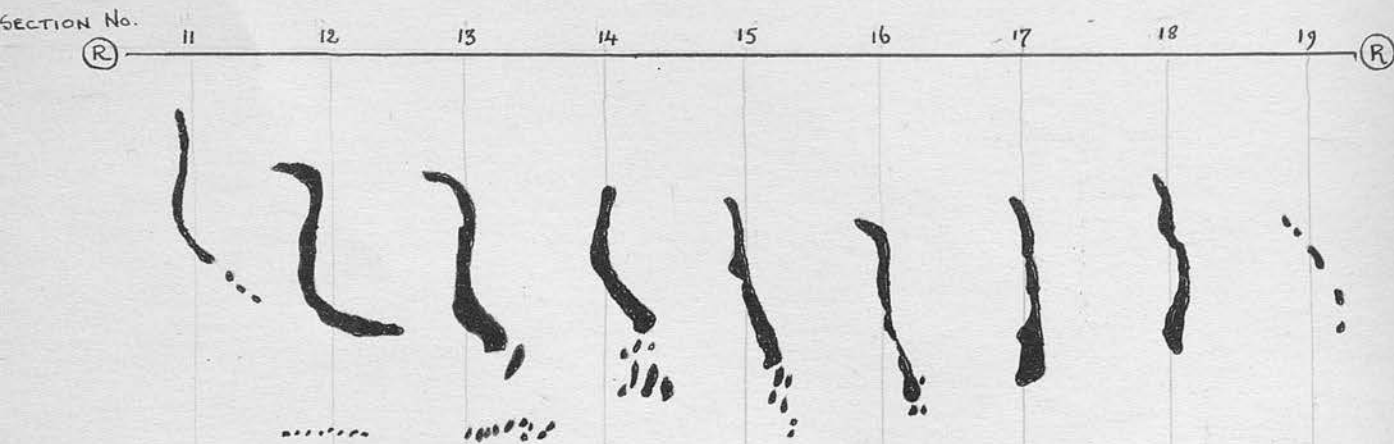


FIGURE 2.



TRACINGS OF CLAUSTRAL OUTLINES TO SHOW CHANGE IN FORM.
(VERTICAL DISTANCE FROM REFERENCE LINE (R) CORRECT).
TRACINGS ARBITRARILY SPACED $\frac{3}{4}$ " APART.

masses were found near the apex of the claustrum.

Figure (1) shows a plane projection of the claustrum on the lateral profile of the hemisphere. On account of the depth at which the claustrum is situated this drawing shows only the general form of the structure in lateral view. Including both compact and fragmented zones, the claustrum has an irregular shape. It has some resemblance, as was pointed out by Randaccio (1882), to the squamous portion of the temporal bone of a foetus, the "spur" (Randaccio) corresponding to the zygomatic apophysis.

DISCUSSION.

It is obvious from the above description that the claustrum may be divided into two parts: a dorsal (compact) part, the claustrum as commonly described, and a ventral (fragmented) part composed of a mass of grey islands scattered below the compact claustrum. The claustrum parvum of Landau is, for the present, included in the ventral claustrum.

The compact (dorsal) claustrum has been repeatedly described, but the descriptions frequently appear to have been based on examination of relatively few macroscopic preparations and are, in some cases, distorted by the views of their authors concerning the relationships of the claustrum to neighbouring formations. Several works, however, contain series of macroscopic sections (in various planes) showing the claustrum in detail:- Dejerine (1895), Jelgersma (1940), Foix and Nicolesco (1925). Landau (1918) published a

diagram of the claustrum which is in general agreement with figure (1). Campbell (1905) prepared projective diagrams of the claustrum in various species, but does not appear to have published them.

In discussing the macroscopic relation of the claustrum to neighbouring structures it is necessary to recognise the limits imposed by the present method of investigation, which merely emphasizes the distinction between grey and white matter. Since the claustrum is a macroscopic entity, its general form and topographic relations may be legitimately studied by this method, but no conclusions can be reached regarding its connections or "significance". Notwithstanding this obvious fact dogmatic pronouncements have been made on such matters founded on similar macroscopic observations.

The following discussion therefore will be confined to certain aspects of the topographic anatomy of the claustrum.

Although the compact claustrum is usually stated to be co-extensive with the insula, it is apparent from the description already given that the correspondence between the two formations is not exact. The discrepancy has been pointed out by various authors: Holl (1902), Brodmann (1909), Landau (1919), Pintus (1930), Macchi (1948). There is dispute as to the extent and number of cyto-architectonic fields which comprise the insular region, and the matter can be more fully and more usefully discussed in histological terms.

The lateral surface of the claustrum shows irregularities which do not, in most cases, closely

follow the convolutions of the insula. This is clearly shown in the series of frontal-vertical and horizontal sections published by Foix and Nicolesco (1925).

The widths of the extreme and external capsules vary considerably, both absolutely and relatively to each other. The extreme capsule is the more variable, and has no resemblance to the stria of Gennari of the calcarine cortex. Unlike the latter it is continuous with the white matter of the hemisphere at its limits.

No macroscopic continuity has been found between the dorsal (compact) claustrum and insular cortex, putamen, amygdaloid nucleus or basal cortex. Kuhlenbeck (1924) mentioned an apparent macroscopic fusion between claustrum and anterior perforated substance. Whitaker (1921) stated that the nucleus lenticularis, claustrum and tail of the caudate nucleus were continuous "below and in front" with the amygdaloid nucleus.

The scattered masses of grey matter lying ventral to the compact claustrum have been mentioned by many authors. Mondino (1885) referred to their variability in individual brains, and only two authors, Brockhaus (1938), and Macchi (1948), have described them as entities. The fragmentation of the "ventral claustrum" has been attributed to the fasciculus uncinatus and to the anterior commissure.

The claustrum parvum was described, and was so named, by Landau (1936, 1937, 1938). He stated that it was situated immediately posterior to the temporal pole, lying in the white matter deep to the cortex of the superior surface of the temporal lobe and therefore

completely independent of claustrum, insula or anterior perforated substance. Traced posteriorly he found that it approached the amygdaloid nucleus and insular claustrum. As the claustrum parvum extends beyond the traditional limits of the insula, its discovery was of considerable importance. The relationship of these various grey masses to one another, to the dorsal claustrum and to neighbouring structures will be considered further in the section on histology.

BLOOD SUPPLY OF THE CLAUSTRUM.

Although it is generally agreed that the claustrum is supplied by branches of the middle cerebral artery, the details of this supply have been disputed.

The matter was raised by Elliot Smith (1919) who claimed that the "lateral striate artery" (figured by him as lying in the region of the external capsule of the human foetal brain) was remarkably constant in position and relations in the various orders of mammals. He considered that this vessel indicated the boundary between palaeo-striatum and hypo-pallium. He further considered that its constancy of position in reptiles and mammals corroborated his hypothesis that a large part of the human corpus striatum was homologous with the reptilian hypopallium, and was therefore cortical in origin.

Older authors; such as Duret (1873) and Beevor (1909), described the claustrum as receiving fine arterioles which penetrated the convolutions of the insula. Shellshear (1920) re-investigated the subject

in the light of Elliot Smith's findings. He ascertained (by injection and ligation experiments) that the claustrum was supplied by a separate and distinct series of five vessels passing through the limen insulae to reach it. These vessels were basal branches of the middle cerebral artery, arising more laterally than the commonly named lateral striate artery. In his experiments he found no anastomosis between the vessels of insular cortex, claustrum or lenticular nucleus.

Bohne (1926) stated that the claustrum was supplied by fine perforating twigs from the pial network of the insula and from terminal branches of the middle cerebral artery. Itabasi (1928) described branches of the middle cerebral artery which pierced the insula to reach the claustrum.

HISTOLOGY AND CONNECTIONS OF THE CLAUSTRUM.

MATERIALS AND METHODS.

A preliminary series of blocks was embedded in paraffin wax, sections cut (10μ) and stained by the following methods: Borrell's Methylene Blue, Einarson's Galloxyanine, Bielschowsky's Silver Impregnation and Krohnthal's Lead Sulphide Impregnation. The metallic impregnation methods above mentioned require treatment of an entire block. As it was desired to compare stained and impregnated sections from the same block these procedures were unsuitable and the following methods were adopted: Landau's Silver Impregnation and Foley's Protargol-Galloxyanine Stain. These have been used throughout the present investigation. Details concerning them are given in the Appendix on Technical Methods.

Three formalin-fixed hemispheres were examined. The first was cut in a macrotome (in the frontal-vertical plane), slices $\frac{1}{4}$ m.m. thick being prepared in serial order, passing posteriorly from the genu of the corpus callosum. A tracing was made, showing the topographic features of each slice, and blocks removed from all zones of the claustrum. The exact locations of these blocks were marked on the tracings, which were subsequently used as key-diagrams for orientation purposes. The macroscopic slices were labelled (A) to (L) inclusive, individual blocks being indicated by Roman numerals. The blocks were cut (at $8-10\mu$) in the frontal plane.

Slices about 5-10 m.m. thick were cut in the

frontal-vertical plane from two other hemispheres. Blocks were removed from regions suitable for the investigation of the relationships between the claustrum and various adjacent structures. Sections were cut from these blocks in frontal, sagittal, horizontal and oblique planes. Tracings were made as before. This series was designated by the letter (S) and Roman numerals.

Most of the blocks showing cerebral cortex were cut in the frontal-vertical plane; the plane of section was not usually perpendicular to the surface and long axes of the gyri. Exact study of the cyto-architectonic features of the insular cortex therefore could not be made. In the figures in this work sections are designated by their reference letter and numeral; their exact location is shown in the key-diagrams. (Appendix 2).

In studying the macroscopic anatomy of the claustrum, the structure was found to have two relatively distinct subdivisions: dorsal (or compact), ventral (or fragmented). This division will be maintained for convenience in the initial histological description.

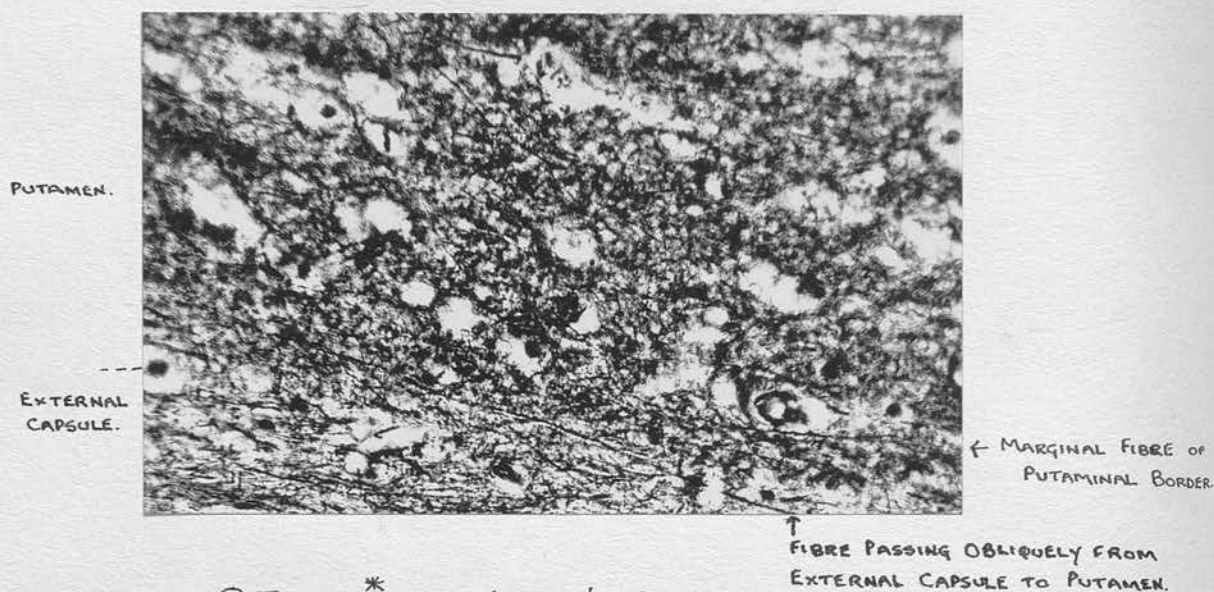
PERSONAL OBSERVATIONS.

(a) Dorsal compact claustrum: Examination of the series of silver-impregnated sections showed that the claustrum was much less clearly defined than in the macroscopic preparations. Under the microscope it appeared as a region containing a relatively dense collection of cell-bodies, and a fairly characteristic

fibre structure. These features constituted an obvious difference between the appearance of the central zone of the claustrum and that of the adjacent capsules. These differences, however, developed gradually rather than abruptly in passing from the claustrum to either external or extreme capsule. The claustrum was better defined in Protargol-Gallocyanine sections, mainly on account of its relative poverty of myelin. Since the claustrum was not sharply delimited, it was decided to take the region between the lateral border of the putamen and the insular cortex as a unit for descriptive purposes. The putaminal-insular region was therefore examined from medial to lateral limits, external capsule, claustrum and extreme capsule being considered in this connection as topographic zones only.

(i) External capsule. The lateral border of the putamen formed the medial and more definite limit of the putaminal-insular region. The putamen was clearly defined (in silver preparations) both by the form and arrangement of its cells, and by its fibrillar structure. The putamen was thus quite distinct from the external capsule under low magnifications. Under higher powers, however the following features were noted: (a) The extreme lateral district of the putamen contained a considerable number of fibres running roughly parallel to those of the external capsule; their diameter was equal to that of the majority of the capsular fibres. (b) Small groups or "strands" of fibres were seen to diverge gradually from the body of the capsular fibres, and to pass into the marginal zone

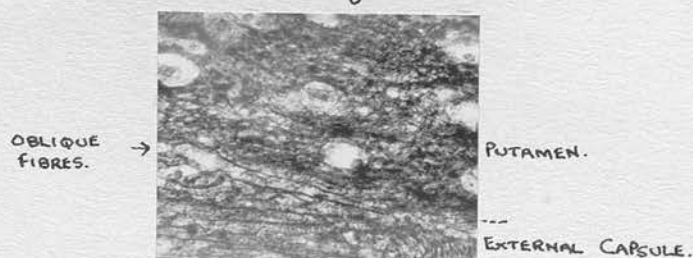
FIGURE 3.



⑤ V. * F.V.S. x 420. LANDAU'S SILVER.

OBLIQUE FIBRES PASSING BETWEEN EXTERNAL CAPSULE AND PUTAMEN

FIGURE 3a.



⑤ XIV. * H.S. x 500. LANDAU'S SILVER.

OBLIQUE FIBRES PASSING BETWEEN EXTERNAL CAPSULE AND PUTAMEN.

*

F.-V.S. = FRONTAL-VERTICAL SECTION.

H.S. = HORIZONTAL SECTION.

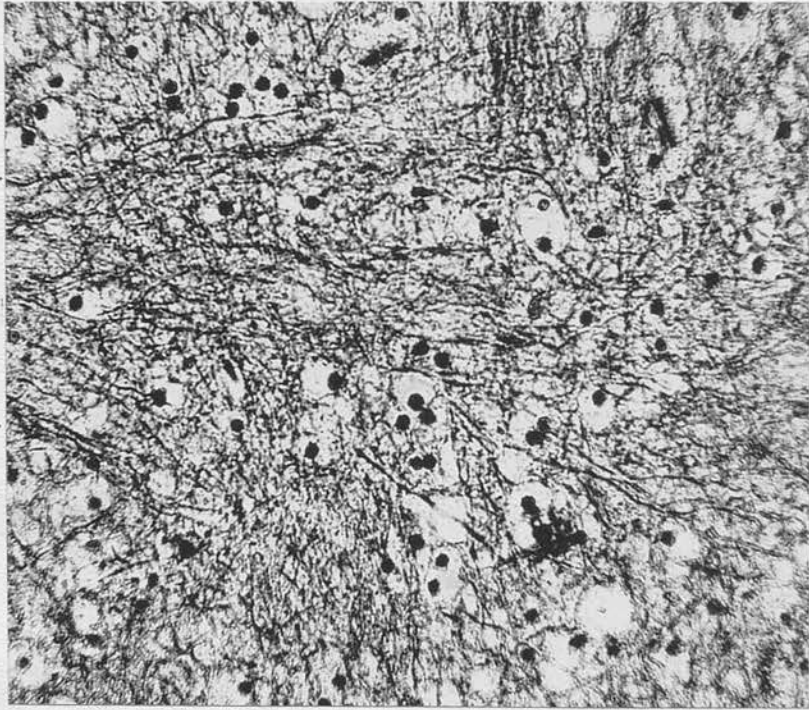
of the putamen. In some cases these divergent fibres contributed to the "marginal" fibres of the lateral putaminal border already mentioned. The passage from capsule to putamen could be traced through several fields. This exchange of fibres was not always noticeable, and was less common on the inferior border of the putamen (Fig.3). (c) In certain places, to be described later, bundles of fibres passed between the superior part of the lateral border of the putamen and the external capsule (Fig.4). (d) Occasionally the region between putamen and external capsule was occupied by a mass of fine fibres, passing in all directions and forming an intricate network.

There is therefore a constant exchange of fibres between the putamen and the external capsule, and although the number of such fibres seen in any one field is usually small, the total number of fibres involved must be considerable in view of the large area of contact between putamen and capsule. The origins (or terminations) of these fibres within the putamen could not be determined.

Apart from this medial transition zone the external capsule had a fairly constant and characteristic structure (Fig.5). It was mainly composed of fibres which were approximately parallel to each other and to the lateral border of the putamen. This parallelism was found in both frontal and horizontal planes. The majority of the fibres ran vertically, but a large number were directed antero-posteriorly approximately in the horizontal plane. Most of the capsular fibres

FIGURE 4.

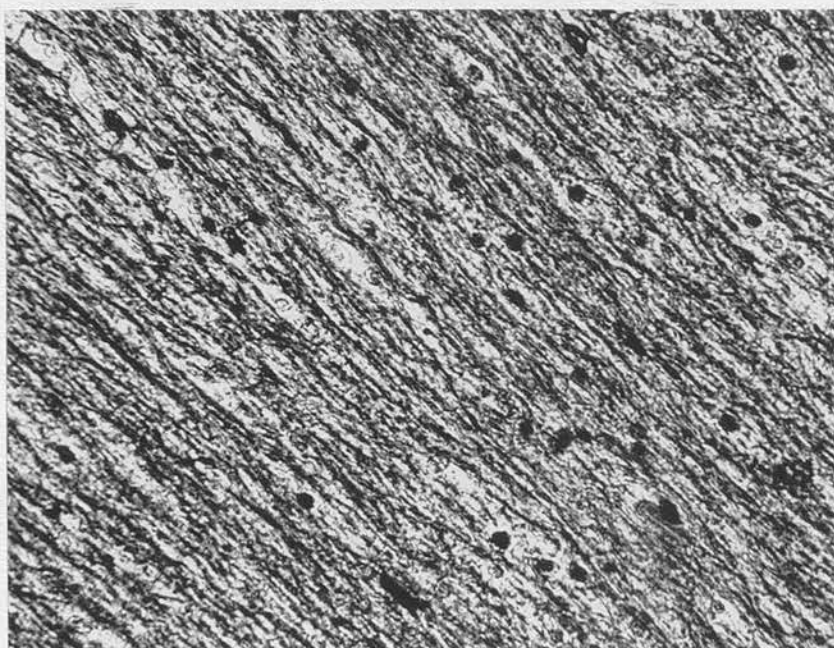
FIBRE-BUNDLE
TRAVERSING
EXTERNAL CAPSULE
BETWEEN PUTAMEN
AND
CLAUSTRUM.



(S) IV. F.-V.S. X 420. LANDAU'S SILVER.

BUNDLE OF FIBRES PASSING ACROSS EXTERNAL CAPSULE
BETWEEN PUTAMEN AND CLAUSTRUM.

FIGURE 5.



⑤ XIV. H.S. x 420. LANDAU'S SILVER.

EXTERNAL CAPSULE SHOWING APPROXIMATELY PARALLEL
ARRANGEMENT OF FIBRES.

FIGURE 5a.



⑤ XIV. H.S. x 500. LANDAU'S SILVER.

OVOID CELL IN EXTERNAL CAPSULE
(INDICATED BY ARROW ↓).

were of moderate diameter. The individual fibres were commonly grouped in "strands". These "strands" were only relatively distinct from one another, as single fibres passed from one such "strand" to others adjacent. The parallelism of individual fibres and of fibre strands was more evident near the putaminal border, as the inter-connections of the "strands" became more obvious in the lateral part of the capsule. Occasionally a vertically directed fibre was seen to bifurcate, one branch continuing along the capsule, the other passing at right angles to it towards the lateral border of the putamen. In some cases these fibres could be traced into the putamen itself, but their relationship to the putaminal cells could not be demonstrated. In the superior part of the external capsule, well-defined groups of fibres were found running transversely from the putamen, across the external capsule, to the claustrum. They could not be traced to putaminal or to claustral cells (Fig.4). Short segments of isolated transverse fibres were found scattered throughout the external capsule at practically all levels.

The external capsule contained fusiform cell-bodies, of varying size, arranged with their long axis parallel to the capsule fibres. Their apical process disappeared within a short distance of the cell-body. Some ovoid cell-bodies were also found (Fig.5a). A few of these had a process which bifurcated near the cell body, the branches proceeding for considerable distances, diverging from each other.

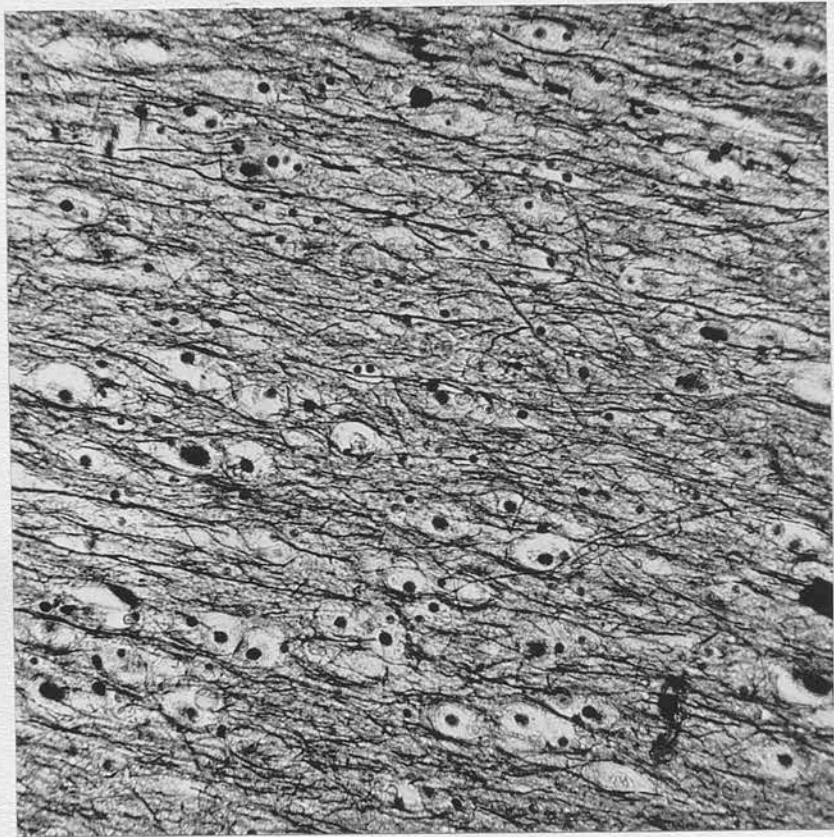
In the more lateral part of the capsule the connec-

tion between adjacent "strands" became more highly developed, so that a retiform arrangement (with oval spaces) was produced. The cellular content of this fibre network increased fairly rapidly on passing laterally, but in most cases there was no sharp transition from the cell-poor capsular region to the cell-rich claustral region. Capsular "strands" and individual fibres passed obliquely, over a distance of several high-power fields into this retiform arrangement, whose inter-spaces were larger, and mostly occupied by cell-bodies. This region represented the macroscopic claustrum. In spite of the usually gradual change from capsular to claustral regions there was little resemblance between the structure of the external capsule and that of the central part of the claustrum. In Protargol-Gallocyanine sections the claustrum was better defined, owing mainly to the relative poverty of myelin, and greater content of nuclei.

(ii) The claustral region, therefore, is distinguished from the external capsule by the following features: a denser population of cell bodies (of more varied type), the arrangement of its fibres, and by poverty of myelin.

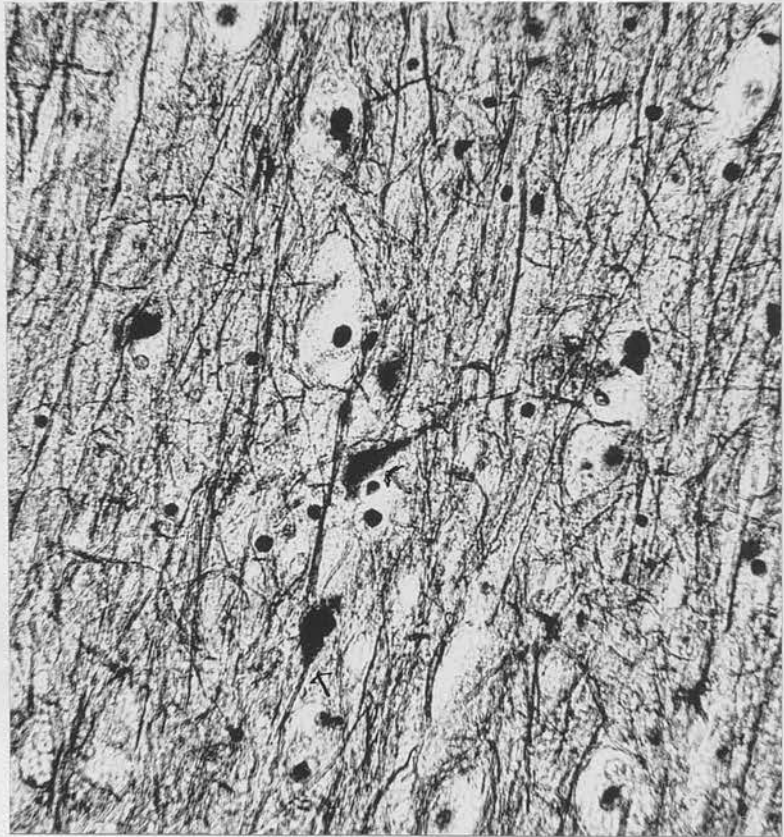
As the "strands" of the external capsule were followed into the claustral zone, they gradually formed a more open network, mainly composed of finer "strands" and, in many places, of individual fibres. These fibres, mostly of fine or of moderate diameter, tended to run parallel to each other, but this became less obvious in the central part of the claustral zone. The bodies

FIGURE 6.



⑤ XIV. H.S. x 255. LANDAU'S SILVER.
FIBRO-CELLULAR RETICULUM OF CLAUSTRAL ZONE.

FIGURE 7.



⑤ XIV. H.S. X 420. LANDAU'S SILVER.

FIBRO-CELLULAR RETICULUM OF CLAUSTRAL ZONE
SHOWING CHARACTERISTIC APPEARANCE - TWO TRIANGULAR
CELLS IN CENTRE OF FIELD.

of the claustral cells lay in the oval or irregularly-shaped inter-spaces of the fibre-network. Some thick isolated fibres traversed the claustrum in all directions. These fibres could be followed for considerable distances, and maintained a constant course. They were closely related to the spaces containing the claustral cells. In such situations they formed a segment of the boundary of the inter-space, developing a shallow curve before resuming their direction. They impregnated heavily with silver, thereby exaggerating the reticular appearance. They did not appear to give off collaterals in the vicinity of the claustral cell bodies (Fig.6).

Where the claustral region was narrow, the cell bodies were usually fusiform or ovoid; where the claustral region was broad, the cells were more varied: fusiform, ovoid, triangular and polygonal types being found (Fig.7). Fusiform cells seemed to be more numerous near the capsules. The other types had an apparently random distribution. There was no evidence of stratification such as is found in the cortex. The mutual relationships of the various types of claustral cell could not be determined. The different forms of cells were characterised by the following features:

Fusiform and ovoid cells (Figs.8, 9). These were commonly oriented with their long axis parallel to the vertical axis of the claustrum. The alignment of the claustral fusiform cells consequently differed from that of the fusiform cells found in the deepest layer of the insular cortex. The fusiform and ovoid cells gave off processes from their superior and inferior poles. These

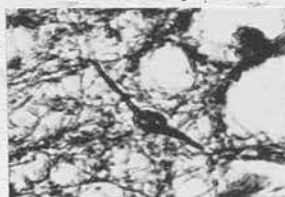
FIGURE 8.



← FUSIFORM
CELL

① V, F.-V.S. x 425. LANDAU'S SILVER
FUSIFORM CELL - CLAUSTRAL
ZONE.

FIGURE 9.



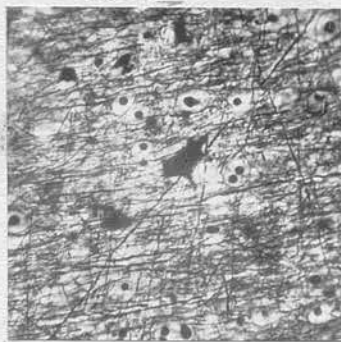
① III, F.-V.S. x 425. LANDAU'S SILVER.
OVOID CELL - CLAUSTRAL
ZONE.

FIGURE 9a.



(H) III. F.-V.S. x 500. FOLEY'S STAIN.
TRIANGULAR CELL-CLAUSTRAL
ZONE.

FIGURE 10.



(S) XXI. OBLIQUE S. x 500. LANDAU'S SILVER
POLYGONAL CELL-CLAUSTRAL ZONE.

processes appeared to run vertically, but could only be followed for a short distance. In some well-impregnated examples of ovoid cells, dendrites came off from each pole, and shortly afterwards began to ramify, then disappearing; the axon arose from the cell body near one pole, followed a curved course and could not be traced for any distance. In sections stained with Protargol-Gallocyanine the nucleus was found to occupy the greater part of the cell body: it was elongated, and stained deeply and uniformly.

Triangular cells (Fig.9a). These gave off processes from each pole, the processes passing in all directions. Their axons were seldom impregnated and could not be traced for more than a very short distance from the cell-body. The cells were of various sizes and shapes. Their nuclei (in Protargol-Gallocyanine preparations) were large and vesicular. They usually had a sharply defined nuclear membrane, a peripheral ring of chromatin and a central nucleolus. The Nissl substance was formed by an agglomeration of small particles and showed no characteristic features.

Polygonal cells (Fig.10). These were frequently oblong, had no constant orientation and were most common in the central part of the claustral zone. Their processes passed in all directions, soon vanishing in the claustral reticulum. Their axons failed to impregnate. Their nuclei resembled those of the triangular cells.

In the ventral part of the anterior portion of the claustral zone, areas were found which contained very

few cell-bodies and many parallel fibres. These fibres were mainly directed vertically. These areas, which were continuous at either side with typical claustral reticulum, represented the transition between the dorsal (compact) and the ventral (fragmented) claustrum.

The superior part of the claustrum had no special features, except for the presence of groups of transverse fibres already described. As the claustral zone narrowed towards its apex, the cell population dwindled, fusiform cells predominated and the fibres of the claustral reticulum assumed a parallel arrangement similar to that of the adjacent capsules. No detached "islets" of claustral reticulum were found in this situation.

In passing laterally in the claustral region the cells became less numerous, the reticular spaces more oval and smaller, and the parallelism of the fibres became more obvious. Thus the lateral claustral region was not sharply differentiated from the adjacent extreme capsule.

(iii) The extreme capsule. The fibres of the medial part of this zone were mainly oriented vertically; many passed obliquely into the claustral reticulum. In the more lateral parts of the capsule, the fibres had a less orderly arrangement, and were more variable in diameter. The radial bundles of the insular cortex were found to curve gradually into the extreme capsule, finally assuming an approximately vertical direction. In certain situations, however, the radial bundles continued through the extreme capsule, entered the claustral zone and

became lost in its reticulum.

Cell bodies were scattered irregularly throughout the extreme capsule. In the medial part they tended to be fusiform, lying with their major axis parallel to the vertical fibres. Fusiform, triangular and polygonal cells were found in the lateral part of the capsule. The demarcation between extreme capsule and insular cortex was less distinct than that between putamen and external capsule.

As was noted in the macroscopic studies, both external and extreme capsules varied greatly in width. Although both capsules contain many cell bodies, these were dispersed. No accumulation of these cells (such as would constitute a cellular "bridge") was found between putamen and claustrum or between claustrum and insular cortex. The relatively dense cell population of the claustrum was everywhere separated from putamen and insula by the sparsely cellular capsular zones.

(b) Ventral (fragmented) claustrum. The masses of grey matter ventral to the dorsal compact claustrum will be described together, then the claustrum parvum (of Landau) and finally the relationships between dorsal and ventral claustrum and between the latter and certain neighbouring structures (cortex, amygdaloid nuclei).

As has been already mentioned, areas were found in the anterior part of the ventral border of the compact claustrum which contained few cells and many fibres. Most of these fibres were parallel to each other and to the fibres of the external capsule. Alternating with such areas were regions rich in cells showing the typical

FIGURE 11.

FIBRE-BUNDLES. | CLAUSTRAL RETICULUM. |



↑
↑
BUNDLES OF VERTICALLY DIRECTED FIBRES.

① ✓. F.-V.S. x 54. LANDAU'S SILVER.

"SERRATED" VENTRAL MARGIN OF DORSAL CLAUSTRUM, SHOWING
AREAS OF CLAUSTRAL RETICULUM BOUNDED BY FIBRE-BUNDLES.

claustral reticulum. These serrations of the claustral margin represented the origin of the "islands" and "streaks" of the ventral claustrum (Fig.11).

These "islands" and "streaks" were well defined under low magnification, because they were bounded by masses of fibres curving around them. Many fibres entered the ventral border of the "islands", becoming lost in their reticulum. Under higher magnification those groups of fibres which appeared to delimit the islands were seen to be separated from the cells of the latter by a network of finer fibres passing in all directions between the fibre bundles and the "islands" proper (Fig.11a). The appearances suggested the occurrence of axo-dendritic synapses. This feature was most noticeable in the case of the "islands" lying immediately ventral to the compact claustrum in the narrow region between insula and hippocampal lobule, the "insulo-hippocampal strait". The reticulum in the interior of the "islands" resembled that of the dorsal (compact) claustrum. It was traversed in all directions by solitary coarse fibres. As in the dorsal claustrum, these coarse fibres were closely related to the interspaces of the reticulum, forming a segment of the boundary, whilst maintaining their general direction. No collateral branches were given off by these fibres in the vicinity of the cell-bodies contained in the inter-spaces.

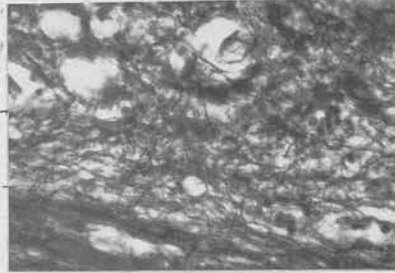
The cell-bodies lay in the interstices of the network, whose finer fibres were closely related to them. These fibres formed part of the deeply-impregnated

FIGURE 11a.

ISLAND OF
"VENTRAL"
CLAUSTRUM

FIBRE-
NETWORK

COMPACT FIBRE
BUNDLES.



① V. F.-V.S. x 500. LANDAU'S SILVER
BOUNDARY OF CLAUSTRAL "ISLAND"
SHOWING FIBRE-NETWORK BETWEEN
COMPACT BUNDLE AND "ISLAND"



FIGURE 12.

③ X. F.-V.S. x 90. LANDAU'S SILVER.
"STREAK" OF VENTRAL CLAUSTRUM.

alveolar boundary; in many cases they disappeared abruptly close to the cell-bodies.

The cells were of the types found in the dorsal claustrum: fusiform, ovoid, triangular, and polygonal. The fusiform cells were less prominent in the "islands" than in the compact claustrum. The cells varied in size, and had an apparent random distribution and orientation.

More anteriorly, in the dorsal part of the white matter of the temporal lobe the ovoid "islands" were replaced by narrow "streaks" or "rays" (Fig,12). These were usually orientated with their long axes supero-medially or supero-laterally. These "streaks" were composed of reticulum with claustral features: cellular polymorphism, random distribution of cell types, and "alveoli" bounded by heavily impregnated fibres. The fibres adjacent to this reticulum ran parallel to the "streaks" and some fibres passed into the reticulum, either by branching at right angles or by gradual divergence. Protargol-Gallocyanine staining showed the "streaks" to be poor in Myelin. They therefore stood out clearly against the surrounding mass of fibres.

Although the claustrum parvum (of Landau) is plainly visible to the naked eye, it was badly defined by the silver impregnation method. This demonstrated it as an indistinct concentration of cell-bodies, varying considerably in depth and extending in an irregular sinuous line between the medial and lateral portions of the superior temporal cortex. The cells, mainly

triangular and polygonal in type, were sometimes enclosed in spaces bounded by heavily impregnated fibres, but this arrangement was less obvious than in the "islands" and "streaks". No definite organization of nerve fibres was found in the vicinity of the claustrum parvum, which was traversed obliquely by single thick "fibres"; these did not usually end within it. Cell-bodies were scattered throughout the adjacent fibre-mass both ventral to the claustrum parvum and between it and the super-jacent temporal cortex. These were mostly small triangular cells.

As the claustrum parvum was followed posteriorly in a series of sections it was seen to be interrupted, in its central portion, by the obliquely-disposed "rays" already described. Protargol-Gallocyanine stains showed that the claustrum parvum was poor in myelin; in these preparations the formation was fairly well defined. It had an irregular ventral and dorsal border, and extended horizontally in a continuous band. It was not broken up by discrete bundles of fibres. The cells of the claustrum parvum were mainly triangular and polygonal. They resembled those of the "streaks", "islands" and compact claustrum.

In sections stained by Foley's method the claustrum parvum was not clearly separable from the adjacent "rays". The intervening zone was poorer in cell-bodies and richer in myelin than either of these formations. No fibre-bundles were seen to pass between claustrum parvum and "rays" in Landau's silver preparations.

At its lateral and medial ends and superior border

the claustrum parvum gradually became richer in myelin and its cells became more sparse. These were the transition regions between it and the deep surface of the temporal cortex. No bands of cells united the two structures, and the arrangement of the fibres in the transition region was disorderly. There was no obvious fibre connection between claustrum parvum and the neighbouring parts of the temporal cortex.

"Islands" and "rays" were situated near the deep surface of the cortex in several places. This cortex was not linked to the "islets" by cell groups; no fibre-bundles were seen to extend between the formations. The relationship between the detached cell groups constituting the "islands" and the temporal cortex appeared to be merely topographical. The intervening region resembled that found between the ends of the claustrum parvum and the temporal cortex.

Some of the detached cell groups of the fragmented claustrum closely approached the lateral amygdaloid nuclei. The intervening zones contained a dispersed population of cells which could not be definitely allocated either to claustrum or to amygdala. No particular arrangement of fibres was found in these transitional regions.

There was a close histological resemblance between the various "islets" of grey matter which lie ventral to the compact claustrum. All showed cellular polymorphism and apparent absence of ordered disposition of cells, contained the same cell types, and had a similar arrangement of fibres. It would

be impossible, with the methods employed in the present investigation, to distinguish between them on histological grounds. No important differences were found between those groups of cells which were adjacent to the cortex and those in the depths of the fibre-mass of the temporal lobe. The cell groups near the cortex were not joined to it by cellular bridges, nor could connecting fibre-bundles be demonstrated. The accumulations of cells constituting the "islands" and "streaks" varied considerably, both in size and situation, from brain to brain. Accordingly they will not be discussed individually, and will not be regarded as "dependencies" of the cortical fields to which they are adjacent. The claustrum parvum of Landau contains the same types of cells as the "islands" which it closely resembles. It is distinguished by its constancy of topographical position. No definite orientation of its cells could be determined in frontal-vertical, or horizontal sections and it was interpenetrated posteriorly by the other "islands". It is therefore provisionally allocated to the fragmented claustrum.

For the above reasons the numerous isolated cell-masses situated ventral to the compact claustrum will be considered to form a class of histologically similar formations.

The relationship, both of continuity and of

histological resemblance, between dorsal (compact) and ventral (fragmented) claustrum remains to be reviewed. Both structures showed the same cellular types arranged in apparent disorder, and both had a similarly-formed fibre-reticulum. The "islands" contained relatively few fusiform cells as compared with the compact claustrum. This was the only striking difference. As regards continuity, the origin of at least some portions of the fragmented claustrum from the serrated ventral border of the compact claustrum has already been described. Traced anteriorly the ovoid "islands" were replaced by "streaks" and these by the claustrum parvum of Landau. To what extent these "islands" and "streaks" are actually completely separated from the compact claustrum by fibre-bundles, and to what extent they represent a cross-section of a group of cells extending from the dorsal claustrum cannot be definitely stated. The question could only be settled by serial section and reconstruction methods. In view of the close histological resemblance between dorsal claustrum and the ventral cell-groups, and in the absence of detailed knowledge regarding the fibre connections of either formation, they may be taken together as forming a homogeneous structure.

Before proceeding to discuss the literature dealing with the histology and connections of the claustrum, the results of the present investigations will be summarized:

(a) Dorsal (compact) and ventral (fragmented) claustrum resembled each other closely in cellular form, and in arrangement of cells and fibres. They were considered to form a homogeneous structure.

(b) The region between lateral border of putamen and insular cortex was found to contain three zones, which were not sharply delimited from each other. The central zone, with a relatively dense cell population and a complex fibre reticulum, represented the macroscopic dorsal claustrum. The medial and lateral zones with a scanty dispersed cellular content and a predominantly parallel (mainly vertical) arrangement of fibres represented respectively the macroscopic external and extreme capsules.

(c) Each zone exchanged fibres with its neighbours, both by transverse fibres and by lateral or medial divergence of the parallel fibres.

(d) The external capsule exchanged fibres with the putamen, the extreme capsule with the insular cortex. The exact origin or termination of these fibres could not be determined.

(e) The claustrum contained fusiform, ovoid, triangular and polygonal cells. The fusiform cells appeared to predominate in the narrower regions of the broader parts; they were less evident in the central regions of the dorsal claustrum and in the ventral claustrum. The fusiform cells were mainly orientated with long axis parallel to the vertical axis of the claustrum. The other types of cells showed no constancy of situation or orientation.

(f) The processes of the claustral cells could not be traced for any distance from the cell body. Therefore no connections between claustral cells and those of adjacent formations were demonstrated.

(g) No cellular "bridges" were found between dorsal claustrum and neighbouring structures. No "bridges" joined the cell groups of the ventral claustrum to the adjacent cortex, although in some cases they closely approached it.

(h) Ventral claustrum and amygdaloid complex. Islands of the ventral claustrum closely approached the lateral amygdaloid nuclei. The cells in the intervening zone could not be definitely allocated to either formation.

DISCUSSION.

(a) Cell types. The most detailed account available is that given by Pintus (1930). He stated that the claustral cells were polymorphous, that no particular type of cell predominated, and that the claustrum could not be divided into layers on a basis of cellular arrangement. He classified the cells as follows: pyramidal cells (of various sizes) triangular cells, quadrangular cells, polyhedral (pentagonal) cells, unipolar, fusiform cells and bipolar cells. He added that there were an infinite number of intermediate and transitional forms. He was unable to ascertain definite connections for any of the above types of cells; his classification therefore merely emphasised the polymorphism of the claustral cells. He considered that there were two principal kinds of cells; those with short axons (more numerous) ending close to the cell-body and those with long axons (mainly directed along the vertical axis of the claustrum). He traced

some of these long axons towards the external and extreme capsules.

Cajal (1902) maintained that the claustrum was composed of deep star and spindle cells. He pointed out that there were no true pyramidal cells, as the cells of that form always lacked the radial shaft directed towards the surface (of the cortex). He stated that the claustral cells had no constant orientation, but that many cell-processes extended parallel to the (insular) cortex. He divided the cells of the claustrum into two main groups.

(i) Large triangular or stellate cells. These gave off four, five, or more repeatedly branching dendrites, which extended for long distances in all directions, ending within the claustrum. In some cases their axons passed into the vicinity of the fibro-cellular layer (extreme capsule). He believed that the cells with axons so directed were star cells with long axis-cylinders.

(ii) Medium-sized and small cells. These had smaller and shorter processes, some arranged parallel to the plane of the claustrum. They had a slender axis-cylinder which gave off some collaterals. In spherical cells the axon appeared to break up into a loose ramification. Other cells showed no axonal ramification; the axon extending into a medullary fibre. He found no vertical spindle cells, (i.e. with axons directed towards the cortex). In a later work (1911) he described the claustrum as a zone of grey matter where large star cells were found.

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Macchi (1948) stated that the "para-insular" (i.e. dorsal claustrum) showed cellular polymorphism, fusiform cells predominating in the thinner parts, fusiform cells, slender triangular cells (with long apical dendrites and two "bushes" of basal dendrites), ovoidal, squat triangular and polygonal cells being found together in the thicker parts. He described the claustral cells as having no constant orientation, except that the long axis of the fusiform cells was parallel to the dorso-ventral axis of the claustrum. He found that the cells of the claustrum varied greatly in size. In agreement with Cajal (1902) he drew attention to the fact that the major axis of the claustral fusiform cells was perpendicular to that of the fusiform cells of the insular cortex. He found the same cytological features in the various subdivisions of his "Area claustrale ventrale" (approximately corresponding to the ventral or fragmented claustrum), except that in these fusiform cells were less numerous. Mondino (1885) gave a similar description of the cells of the claustrum. He also remarked that spindle-shaped cells tended to be found at the periphery of the claustrum and that, on the whole, such cells became more elongated the more peripheral their situation. He found it difficult to follow the processes of the claustral cells for any distance. Von Bechterew (1899) stated that the claustrum was almost entirely composed of spindle-cells, as did Kuhlénbeck (1924). The latter author emphasized the resemblance between the fusiform cells of the claustrum and those of the insular cortex, a point earlier made by Randaccio (1882).

(b) Details of cytoplasm and nuclear structure of claustral cells. Pintus (1930) described the chromatin as usually scanty, and remarked that the tigroid bodies had no definite arrangement and stained less deeply than those of the cortical cells. According to him the neuro-fibrillae had an alveolar disposition; the nucleus was frequently fairly large, round, vesicular, and occupied about a third of the cell. The nuclear membrane was well defined, the nucleolus central or peripheral.

(c) Histochemical characteristics of the claustrum. Several authors have drawn attention to the difficulty of staining or impregnating the claustrum: Cajal (1902), Weigert (1910), Landau (1939). This is probably due to some physical or chemical peculiarity of the claustral cells, but little work has been done on the subject. Spatz (1922) found that the claustrum gave a feeble reaction for iron (ammonium sulphide method). The intensity of the reaction was equal to that given by the amygdaloid nucleus, and approximately equal to that of the cerebral cortex. Pintus (1930) demonstrated fats and lipoids in the cells.

(d) Fibre-structure of the claustrum. Pintus (1932), using silver impregnation methods, described three zones in the "para insular" (i.e. dorsal) claustrum. In the first and third the fibres were parallel to the fibres of the extreme and external capsules, to which the zones were respectively adjacent. The intermediate (second) was reticular and less compact. He traced fibres from this intermediate zone towards the capsules but was unable to follow them beyond the middle

of the peripheral zones. He found a similar arrangement in Weigert-Pal preparations: both transverse and longitudinal fibres were seen. The transverse fibres did not bifurcate or give off collaterals. In the margins of the claustrum he described fibres which ran for some distance parallel to the fibres of the capsules and which finally curved into the claustrum, there disappearing.

The relationship between the radial bundles of the insular cortex and the extreme capsule has been disputed. In the present study, some of these bundles were found to curve into the extreme capsule, eventually running parallel to its fibres; others passed through the capsule and merged with the claustral reticulum. Landau (1939) claimed that the radial bundles of the insular cortex did not pass beyond the extreme capsule and therefore did not traverse the claustrum. On the other hand Berlucchi (1927) demonstrated fibres passing between insular cortex and claustrum in the cat.

Before discussing the fibre-connections of the claustral cells, it is necessary to investigate the question of continuity between the cell-mass of the claustrum and that of neighbouring formations. These "grey connections" may be defined as collections of cell-bodies of density approximately equal to that found in the claustrum itself, extending from it to adjacent "grey" masses; since dispersed cells are found amongst the fibres surrounding the various regions of the claustral zone, this definition is of some importance. It will be recalled that, in the investigation of the macroscopic sections, no "fusion" was found between the

dorsal claustrum and any other structure; certain "islands" of the ventral claustrum appeared to be continuous with the amygdaloid complex. Microscopic examination, of course, gives more definite information. The "grey connections" of the dorsal and ventral claustrum will now be reviewed.

(i) Dorsal claustrum and insular cortex. No cellular "bridges" were found in the present investigation. The cells of the extreme capsule were dispersed and the cell population of the capsular zone was less than that of claustrum or insular cortex. These capsular cells have been described by several authors. Cajal (1902) called the extreme capsule the "fibro-cellular layer". Mondino (1885), Spiegel (1919), Landau (1919), and Macchi (1948) denied the existence of cellular continuity between claustrum and insula. Brodmann (1909) considered the claustrum to be a cortical layer, but based this opinion on cyto-architectonic relationships. It should be noted, as pointed out by Landau (1939), that the claustrum does not fuse with the cortex at the limits of the insula, as would be expected were the external capsule an intra-cortical fibre-lamina corresponding to the stria of Gennari of the calcarine cortex. Cajal (1902) did not consider that the claustrum formed part of the insular cortex.

(b) Dorsal claustrum and basal cortex. No evidence of fusion was found in the present study. Landau (1923) stated that the claustrum "touched" the substantia perforata anterior, but gave no further details. Von Economo (1929) described claustral "streaks" which pene-

trated the cortex of the lateral olfactory gyrus (area FK).

(c) Dorsal claustrum and putamen. No evidence of continuity was found. The external capsular cells described by Spiegel (1919) and Berlucchi (1927), are dispersed and do not form cellular "bridges" between the two formations. The claustrum is not continuous with the nucleus subputaminalis (Ayala, 1915, 1924).

(d) Dorsal claustrum and amygdaloid complex. No evidence of fusion found. Many authors: von Bechterew (1899), Landau (1918, 1923), Spiegel (1919), Whitaker (1921) and Kuhlenbeck (1924) refer to continuity between claustrum and the amygdaloid nuclei. Where the above authors give a sufficiently detailed description, the connection mentioned is found to depend on claustral "streaks" and "islands" and therefore does not involve the dorsal claustrum. Macchi (1948) in his extended investigation, attributed the continuity between claustrum and amygdaloid complex to his "Area Claustrale Ventrale" (i.e. approximately ventral or fragmented claustrum).

In view of the histological similarity between the components of the ventral claustrum, and their inconsistency in size, form, and situation, it is unnecessary to discuss their individual relationships to other grey formations.

(e) Ventral claustrum and cortex. The temporal cortex adjacent to the ventral claustrum was elaborately described by Rose (1928) and by Brockhaus (1938). They produced little evidence for fibre connections between

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their fields and the underlying claustrum, and their parcellations have yet to be confirmed by other methods. Brockhaus emphasized that in most cases the claustral cells were separated by a cell-poor layer of fibres from the overlying cortex. Rose tended to stress the continuity between claustrum and cortex. He noted that the claustrum extended beneath the superior cortex of the temporal lobe and therefore included this cortical area in the insular region as the "Lobulus Temporalis Insulae" (Fields ai 9. and ai 10). In general it may be said that the ventral claustral complex lies under piriform, and especially anterior piriform, cortex (Niemer and Papez, 1945).

(f) Ventral claustrum and dorsal prepiriform cortex. Macchi (1948) described fusion between his "claustrum prepiriforme dorsale" and the dorsal prepiriform cortex - a region including the olfactory trigone and the dorsal part of the lateral olfactory gyrus. Von Economo (1929) described groups of claustral cells which penetrated the following cortical areas: FK (lateral olfactory gyrus) and IA (area praecentralis insulae).

(g) Ventral claustrum and amygdaloid complex. The close relationship between these two formations was recognised by Mondino (1885); Pintus (1931) described them as linked by cellular bridges. The ventral claustrum was usually stated to be closely adjacent to the lateral border of the "amygdaloid nucleus". The more recent division of the amygdaloid complex into a large number of constituent cell-masses has necessitated

a more detailed examination of claustrum-amygdaloid relationships. This was undertaken by Brockhaus (1938, 1940) who differentiated many subdivisions of claustrum and amygdala. Unfortunately his second paper (1940) is not available in this country. Macchi (1947, 1948) also described many individual cell-groups in the ventral claustrum, but did not define the precise amygdaloid nuclei to which they were related. It may be said that the ventral claustral groups are adjacent to, and at points continuous with, the baso-lateral amygdaloid nuclei.

From the above considerations it appears that the claustral zone is linked by cellular "bridges" to the cortex in the region of the olfactory trigone and to the baso-lateral amygdaloid nuclei.

In the section on macroscopic anatomy it was pointed out that the claustrum was not exactly co-extensive with the insula, if the latter were regarded as being bounded by the circular sulcus. This discrepancy has been noted by many authors. The question now arises whether the insular region, as delimited by cytoarchitectonics, shows more exact correspondence with the extent of the underlying claustrum. Unfortunately the authors who made a detailed investigation of insular cytoarchitecture (Brodmann, 1909; Rose, 1928) accepted Meynert's doctrine, and consequently regarded the presence of the claustrum as the main distinctive feature of the insular region. Rose, in particular, extended the insular region to include all cortical areas superjacent to the claustrum. Their studies therefore

TABLE 1.

Principal Components of External Capsule.

COMPONENT	ORIGIN	TERMINATION	POSITION IN CAPSULE	FUNCTION
Fasc. Longitudinalis Superior.	Frontal Cortex (Lateral Surface)	Cortex of T1, T2. Insula, Parietal & Occipital Lobes; Claustrum.	Superior	Association
Fasc. Longitudinalis Inferior.	Occipital Cortex (Medial & Lateral)	Cortex of Temporal Lobe; Hippocampal Lobule.	Posterior Inferior Third	Association
Fasc. Uncinatus.	Frontal Cortex (Orbital Surface)	Cortex of Uncus & T, T2 (Ant. Pt.)	Anterior inferior	Association
Occipito. Frontal Fasciculus.	Occipital Cortex.	Frontal Cortex.	"Middle Portion"	Association
Thalamic	Ventral Thalamic Nuclei	Areas 1, 3, 1, 2, 7 & 22 of Cortex	Posterior Superior	Afferent: Somato-Sensory
Meta-Thalamic	Medial Geniculate Body	Auditory Cortex of T1. (11).	Inferior	Afferent: Auditory.
Vestibular	Vestibular Nuclei	Cortex of Temporal Lobe.	Anterior	Afferent: Proprioceptive
Olfactory	Lateral & Medial Olfactory Striae	?	Inferior	"Olfactory"
Anterior Commissure	Contra-Lateral Temporal Lobe & Olfactory Nuclei	Cortex of Temporal Lobe. Olfactory Nuclei.	Posterior	Commissural
Callosal	Contra-Lateral Hemisphere.	?	Diffuse	Commissural
Striatal	Caudate Nucleus and Putamen	?	Medial	Unknown.
Cortical	Pre-Piriform Cortex	Clastrum	Inferior	Unknown (? Autonomic)
Claustral	Clastrum	?	?	Unknown

throw no light on insular-claustral correspondence.

Many authors have subdivided the insular cortex into fields on cyto-architectonic grounds. Campbell (1905) recognised two subdivisions, an anterior and a posterior; the line of separation approximately following the central sulcus of the insula. Later authors have usually accepted this division, but have differentiated a larger number of fields. Thus Brodmann (1909) defined four fields, Rose (1928) described three "regions" with many fields, and V. Economo (1929) five fields. One relevant fact emerges from these investigations: in spite of the variation in the overlying insular cortex, the claustrum is not described as showing correspondingly marked cyto-architectonic differences. It appears to remain relatively constant in histological structure.

In the present study no fibre connections between claustral cells and adjoining "grey" formations have been demonstrated. The close relationship between the claustral and the neighbouring capsular zones, involving a constant exchange of fibres, has been emphasised. The external and extreme capsules have a complex composition; the analysis of them which follows is based on an examination of the available literature.

External Capsule. (table 1).

(a) Fasciculus longitudinalis superior (arcuate fasciculus of Burdach). According to Pincus (1932) this bundle is situated at the base of the sylvian opercula, external to the fibres of the corona radiata.

It occupies the superior part of the external capsule. Its fibres connect the frontal cortex (lateral surface) with the cortex of the superior and middle temporal gyri and with the cortex of the parietal and occipital lobes. According to Bianchi (1922) the more superficial and inferior fibres enter the claustrum. Pintus (1932) stated that the superior part of the claustrum was "broken up" by its fibres. From his experimental work (monkeys) Bianchi (1922) concluded that there was a reciprocal exchange of fibres between frontal lobe, putamen and claustrum: d'Hollander (1922), after experimental lesions of the parietal lobe (rabbit) found degenerated fibres in the external capsule. Mettler (1935a), working with the Macaque, found degeneration in the external capsule after lesions involving the ventral half of the superior, the whole of the middle, and the dorsal half of the inferior frontal gyri. The claustrum was stippled by degenerated fibres.

(b) Fasciculus longitudinalis inferior.

von Bechterew (1899), quoting unspecified authors, mentioned this bundle as a component of the external capsule, as did Déjerine (1895). According to Pintus (1932) it is an antero-posterior system of fibres, running along the infero-lateral border of the sphenoccipital lobe. Its fibres connect the cortex of the occipital lobe (including the medial surface) with the temporal lobe and the hippocampal and fusiform gyri. It occupies the posterior third of the inferior part of the external capsule. d'Hollander (1922) working with the rabbit found no degenerated fibres in the external

capsule after experimental lesions of the occipital region. Nothing is known regarding the relationship between the claustral cells and the fibres of this system.

(c) Fasciculus uncinatus. This bundle, which is said to be composed of short fibres, occupies the anterior inferior part of the external capsule. Its medial fibres are strongly curved in a U-shape (open laterally), its lateral fibres straight or even concave superiorly. According to Déjerine (1895) the uncinate fasciculus occupies the whole of the external capsule below the level of the pole of the insula. Most authors attribute the fragmentation of the ventral claustrum to this bundle v. Bechterew (1899), Landau (1936), Macchi (1948). Its fibres connected the cortex of the orbital surface of the frontal lobe with the cortices of the uncus and of the anterior parts of the first and second temporal gyri. According to Macchi (1948) there are two groups of fibres, situated approximately at right angles to each other; vertical fibres from hippocampal lobule and temporal lobe (related to the ventral claustrum) and horizontal fibres (connecting insula and frontal lobe). It is uncertain whether the uncinate fibres synapse with the claustral cells.

(d) Occipito-frontal fasciculus. This is said to connect the cortex of the occipital lobe with that of the frontal lobe. It occupies the "middle" portion of the external capsule. Déjerine (1895), Pintus (1932), Macchi (1948).

(e) Ventral thalamic (Somato-Sensory radiation).

Occupies the posterior part of the superior portion of the capsule. It originates in the ventral thalamic nucleus and terminates in the following cortical areas: 4, 3, 1, 2, 7, and 22. The fibres traverse the posterior superior part of the putamen: Hösel (1905), Probst (1905), Környey (1926), Crouch and Thompson (1938). According to Poliak (1932) (in the Macaque) the fibres enter the external capsule, turn dorsally and terminate in the parietal operculum. Some fibres closely follow the upper "spur" (extremity) of the claustrum and penetrate the cortex around the dorsal corner of the sylvian fossa and that lining the sylvian sulcus. The tract conveys tactile sensory impulses. Peele (1942) found degeneration in the external capsule of the Macaque after lesions of areas 1 and 2 and of area 7. Nothing is known regarding relationships between these fibres and the claustral cells.

(f) Metathalamic (geniculo-temporal or auditory) radiation. This occupies the inferior part of the external capsule. According to Poliak (1932), who based his account on the results of experimental work on the Macaque, this tract originates in the medial geniculate body. It enters the most ventral part of the internal capsule (along with the ventral somatic fibres) and passes horizontally or with a slight ventral trend. Piercing the ventral edge of the posterior part of the putamen it traverses the external capsule and ventral "spur" of the claustrum to reach the auditory area of the superior temporal gyrus (area TC or 41). Pfeiffer (1936), quoted by von Bonin (1950), gives a

similar description for man. Poliak used Marchi's method and was unable to determine the relationship between auditory fibres and claustral cells. According to Pintus (1932), in Golgi preparations no collaterals were demonstrated passing from these fibres to cells of the claustrum.

(g) Temporal (projection) fibres. Rundles et al (1938) found degenerated fibres in the external capsule after bilateral temporal lobectomies in monkeys. The fibres seemed to pass from one hemisphere to another in the anterior commissure. These fibres are therefore distinct from the temporal bundle of the uncinate fasciculus. Pintus (1932) mentioned a portion of the corona radiata of the temporal lobe which passed through the "peri-claustral" white matter: the bundle of Türck. It is not known whether these fibres synapse with the claustral cells.

(h) Vestibular (afferent) fibres. In the cat, according to Muskens (1922), the ascending vestibular fibres probably occupy the anterior part of the external capsule. Although the temporal lobe is commonly believed to contain a vestibular receptive area- stimulation of the superior temporal gyrus in a conscious patient has produced "dizziness" (Penfield and Rasmussen, 1950); little appears to be known concerning the vestibulo-cortical or vestibulo-striatal pathways in man. (Van Laere, 1943).

(i) Olfactory fibres. Köl liker (1896) stated that the fibres from the external root of the olfactory tract traversed the tuberculum olfactorium to reach the

sub-lenticular fibres, which joined the external capsule. According to Landau (1923) the medial olfactory stria was closely related to the external capsule, the lateral olfactory stria extending to the base of the claustrum. More recent investigations of the deep connections of the olfactory tract give little information regarding the claustral region. The lateral olfactory fibres are known to reach the prepiriform cortex (Meyer and Allison, 1949) and may therefore be indirectly related to the claustrum, since the latter is believed to be connected with the prepiriform cortex (Macchi, 1948) and with the piriform cortex (Papez, 1945).

(j) Anterior commissure fibres. Many authors have referred to the presence of anterior commissural fibres in the external capsule. In certain animals e.g. cat, the continuity between the two structures is visible to the naked eye. In man the commissure traverses the canal of Gratiolet on the inferior surface of the lenticular nucleus, and is dispersed laterally, so that the relationship is less obvious.

The exact distribution of the anterior commissure has been investigated by experimental methods (in the Macaque) by Fox and his colleagues. (1945, 1948). According to their account, the commissure divides laterally into an anterior and a posterior limb. The minute anterior limb is distributed to the olfactory tubercle, the anterior olfactory nucleus and the olfactory bulb. The large posterior limb is distributed mainly to the middle temporal gyrus; it contains

other fibres which pass either to the inferior temporal gyrus, to the hippocampal gyrus, or to both these areas. The posterior limb enters the external capsule, undergoing torsion, so that the rostral fibres in the commissure are superior and the posterior fibres inferior. The superior fibres in the external capsule are distributed to cortical zones posterior to those connected with the inferior fibres. Lauer, (1945) gave a similar description; he found a ventral branch which "received fibres" from the lateral and basal amygdaloid nuclei and from the external capsule. This amygdaloid component was also described by Foix and Nicolesco (1925).

The majority of the "cortical" fibres of the anterior commissure are related to the temporal cortex, but Mettler, (1935b) found degeneration in the anterior commissure after parietal lesions. This author (1945) stated that certain striatal fibres passed through the external capsule to the commissure.

Winkler (quoted by d'Hollander, 1922) described a component of claustral fibres which reached the commissure by the external capsule. There is no other information as to the relationship between the fibres of the anterior commissure and the cells of the claustrum.

(k) Corpus callosum fibres. Déjerine (1895) described the callosal component of the external capsule as being derived from the middle part of the body of this commissure. The callosal element was also described (from pathological material) by Kodama (1927) and was mentioned by Pintus (1932). The callosal fibres are said to occupy the middle part of the capsule. The

external capsule is usually normally developed in cases of callosal agenesis - Bruce (1890), Stoecker (1912), Déjerine (1895); the capsule was apparently intact in a case of atrophy on the anterior part of the corpus callosum - de Lange (1925). From the evidence provided by such developmental anomalies the corpus callosum does not seem to make a large contribution to the capsule. It is not known whether these fibres anapse with the cells of the claustrum.

(1) Other components. Although Wernicke (1881) denied any connection between the putamen and the external capsule, many authors have described such connections. Apart from the compact geniculo-temporal and ventral thalamic radiations, which pierce the putamen and traverse the external capsule, other fibres have been noted.

Thus Wilson, (1914) and Kodama, (1927) found fine fibres which passed from the external capsule to the putamen. Kodama stated that these were finer than the "fibrae passantes", did not form a compact bundle, and were not limited to the posterior part of the putamen. Mettler, (1945) described "strio-external fibres" which arose from the caudate nucleus and putamen, and passed downwards through the medial part of the external capsule. Some of these fibres (having been joined by pallidal efferents) passed to the homo-lateral stria terminalis, others to the anterior commissure. The relationship between these striatal fibres and claustral cells is unknown. Macchi, (1948) described a connection between pre-piriform cortex and claustrum; this was also demonstrated (in the cat) by Berlucchi, (1927).

TABLE 2.

Principal Components of Extreme Capsule.

COMPONENT	ORIGIN	TERMINATION	POSITION IN CAPSULE	FUNCTION
Fasc. Longitudinalis Superior.	Frontal Cortex (Lateral Surface)	Cortex of T1, T2 Insula, Parietal-occipital Lobes; Clastrum.	Superior	Association
Fasc. Uncinatus.	Frontal Cortex (Orbital Surface)	Cortex of Uncus & T1, T2 (Ant. Pt.) ? Clastrum.	Inferior	Association
Insular	Insular Cortex	? Insular Cortex	Diffuse	Association
Thalamic	Ventral Thalamic Nuclei.	Areas 7, 22. (? 4, 3, 1, 2.)	Posterior	Afferent: Somato-sensory.
Metathalamic	Medial Geniculate Body.	Auditory Cortex of T. (41).	Inferior	Afferent: Auditory.
Cortical	Prepiriform Cortex	Clastrum	Inferior	Unknown. ? Autonomic.
Cortical	Insular Cortex	Clastrum	Diffuse	Unknown.
Cortical	Insular Cortex	Unknown	Diffuse	Unknown.
Cortical	Temporal Cortex	Unknown	Inferior	Unknown.
Claustral	Clastrum	Unknown	Diffuse	Unknown.

Pintus, (1932) stated that the external capsule contained axons of claustral cells, which ran for some distance in the capsule before re-entering the claustrum. The axons of the external capsular cells, according to Berlucchi, (1927) remained in the capsule. Macchi (1948) suggested that some of the fibres of the external capsule were connected with the substantia innominata. Dejerine, (1895) referred to fibres passing from external capsule to insula through the claustrum.

The external capsule, therefore, is known to contain components derived from the following cortical regions: lateral and orbital surfaces of the frontal lobe, the temporal lobe, the pre-piriform cortex, and the parietal lobe (areas 1, 2, 5 and 7).

Extreme capsule (Table 2). Some fibre systems are common to both external and extreme capsules. Since these systems, (marked x) have already been dealt with in some detail they will be only briefly mentioned below.

(a) Fasciculus longitudinalis superior.x After removal of both frontal lobes in monkeys Bianchi (1922) found a degenerated bundle (representing this fasciculus) in the superior part of the extreme capsule. Mettler (1935a) described fibres connecting prefrontal cortex with the claustrum.

(b) Fasciculus uncinatus.x According to Pintus (1932), Mettler, (1935a), and Macchi (1948), fibres belonging to this system are found in the inferior part of the extreme capsule.

(c) Insular association fibres are scattered diffusely in the capsule - Dejerine (1895), Pintus (1932),

Macchi (1948).

(d) Ventral thalamic (somato-sensory) radiation.* Poliak (1932) found degenerated fibres in the extreme capsule after experimental lesions of the ventral thalamic nucleus of the Macaque.

(e) Meta-thalamic (geniculo-temporal or auditory) radiation.* Lesions of the medial geniculate body were followed by degeneration in the extreme capsule - Poliak (1932).

(f) Insular fibres were described in the capsule by Déjerine (1895), Marburg (1927) and Landau (1936). According to Déjerine fibres pass between external capsule and insula, traversing the claustrum "whose deviations (i.e. serrations of lateral surface) they thereby produce".* Mettler (1945) referred to fibres which arose diffusely from the medullary material of the insula and extended to the claustrum. Berlucchi (1927) described similar fibres in the cat. Little appears to be known regarding the connections of the insular projection fibres; in the albino rat they end on the cells of the entopeduncular nucleus. (Krieg, 1947).

(g) Temporal fibres. Rundles et al (1938) found degeneration in the extreme capsule of monkeys following bilateral temporal lobectomies.

As regards the origin of the cortical fibres in the extreme capsule, the ascertained facts are as follows: Mettler (1935a) from experimental work on the Macaque concluded that there was an important fibre connection between type (9) cortex and claustrum, anterior insula and superior temporal gyrus. Peele (1942) found degen-

eration in the extreme capsule (Macaque) after experimental lesions of the following cortical zones: 1, 2, 5, 7. Berlucchi (1927) described in the cat, fibres passing between the prepiriform cortex and the extreme capsule.

(i) Claustal and capsular cells. According to Cajal (1902), Pintos (1930) and Macchi (1948) the claustral cells send axons into the extreme capsule. Berlucchi (1927) demonstrated this in the cat. The latter author stated that the cells of the extreme capsule sent their axons either to the claustrum or to the insula. Cajal (1902) was unable to trace these axons.

From the foregoing analysis of the external and extreme capsules it is obvious that the claustrum (which is everywhere penetrated by fibres belonging to these capsules) is surrounded, and in many cases traversed, by fibre systems of varied functional significance. These may be summarised as follows:

(i) Inter-cortical association systems: fasciculus longitudinalis superior, fasciculus longitudinalis inferior, fasciculus uncinatus, occipito-frontal fasciculus, insular association fibres.

(ii) Inter-hemispherical (commissural) systems: Corpus callosum and anterior commissure.

(iii) Sensory systems: geniculo-temporal (auditory) radiation, ventral thalamic (somato-sensory) radiation, vestibular (proprioceptive) fibres, olfactory afferent fibres.

(iv) Systems of uncertain functional significance:
Claustro-cortical fibres. Striatal fibres. Fibres
from the substantia innominata and from the prepiriform
cortex. Efferent fibres from the claustrum.

It is assumed that the claustrum is connected with
the following structures:

1. The cortex of the frontal lobes, probably of
both lateral and orbital surfaces. The exact areas
concerned are unknown, but a connection with prefrontal
cortex (type 9) appears to be definitely proved.

2. The cortex of the insula (precise regions not
established.

3. The pre-piriform cortex.

4. Possibly the amygdaloid complex, certain
olfactory nuclei and the contra-lateral claustrum.

It now remains to consider the physiological
significance of the claustrum, having regard to its
connections, so far as they are known, and to such
clinical and experimental data as are available.

THE PHYSIOLOGICAL SIGNIFICANCE OF THE CLAUSTRUM.

In attempting a synthesis of the data reviewed in the preceding parts of this work it is important to review the hypotheses which have been put forward regarding the significance of the claustrum. Such hypotheses, although mere conjectures, indicate the interpretation given by the various investigators to the facts known to them.

Many authors have suggested, on anatomical grounds, that the claustrum is concerned with the speech mechanism. This view was held both by Meynert and by Wernicke; it has been advocated more recently by Pintus (1932) and by Landau (1936). Pintus based his opinion on the connection between the claustrum and the cortex of the superior temporal and inferior frontal gyri; he also quoted Wernicke's statement that the claustrum was closely related to the uncinate fasciculus (believed by the older anatomists to connect the "verbo-motor" and "verbo-acoustic" centres). Landau also was impressed by the relationship between this bundle and the claustrum. On the other hand Lockard, (1948), asserted that the superior longitudinal fasciculus contained fibres which interconnected the insula, upper and anterior part of the claustrum and frontal cortex (including area 4 and probably Broca's area) with the occipital and temporal cortex.

Both superior longitudinal and uncinate fasciculi are macroscopic entities, whose cortical connections have been variously described. Each has been reported to be connected with the inferior frontal gyrus, and both are stated to form synaptic connections with the claustral

cells. There is however, experimental evidence that the claustrum is connected with a large part of the frontal cortex, although all the areas concerned are not precisely known (Bianchi, 1922; Mettler, 1935a). The insular cortex is connected with the claustrum, and the capsules contain fibres derived from the parietal and temporal cortex. There is, therefore, evidence for Lockard's statement as regards the cortical connections of the claustrum; but it is doubtful which fibre-bundles establish these connections. At all events it seems probable that the claustrum (or a portion of it) is connected to some at least of the cortical areas associated with the speech mechanism, and that the fibres responsible for such connections reach the claustral zone through the adjacent capsules. Damage to the region between ^{left} insular cortex and putamen (the "quadrilateral space" of Marie) might accordingly be accompanied by disturbance of speech.

Many cases of lesions in this "space" were published during the controversy which followed Marie's formulation of his views on aphasia. The exact extent of these lesions was frequently inadequately described; few authors made any special investigation of the claustrum. The clinical features of these cases varied greatly. Thus Manóia (1912) found destruction of the left external capsule and claustrum in a patient whose speech had been unaffected; while Mingazzini (1901), from his observations, concluded that the "language pathway" ran on the external surface of the left putamen. No definite evidence as to the effect of claustral lesions on speech

can be obtained from the older literature. In a more recent review Nielsen (19₄₆) stated that within the quadrilateral space the external capsule had much to do with language, and that its destruction produced either paraphasia and agraphia, or motor aphasia and agraphia. He could give no information as to the speech disorder produced by claustral involvement. Lesions restricted to the claustrum do not appear to have been observed clinically. Consequently, although certain fibres concerned in the speech mechanism are closely related (topographically) to the claustrum and form synapses with some at least of its cells, the role of the claustrum in speech is unknown.

Randaccio (1882,) Kuhlénbeck (192₄) and Macchi (19₄₈) believed that the claustrum was a part of the olfactory apparatus. Kuhlénbeck postulated this on comparative grounds (considering the claustrum as possibly homologous with the anterior neopallidum of reptiles). Randaccio thought that both claustrum and amygdaloid nucleus were points of concentration for olfactory impressions. Macchi pointed out that the only certain connections of the claustrum were with the olfactory brain. He regarded the claustrum as an integrative centre for stimuli coming from the olfactory and extra-olfactory zones of the pallium. The olfactory circuits are imperfectly understood in man (Brodal, 19₄₇). Recent investigators e.g. Meyer and Allison (19₄₉) did not trace olfactory fibres to the claustrum. Olfactory afferents are known to pass



to the pre-piriform cortex, which is connected to the claustrum. Berkelbach van der Sprenkel (1926) described (in the opossum) fibres passing from the nucleus of the lateral olfactory tract to the claustrum by the stria terminalis. The anterior commissure contributes fibres, some of which may be of olfactory origin, to the external capsule. The information available is inadequate to decide the relationship of the claustrum to the olfactory apparatus.

Völsch (1906, 1911) and Landau (1919) thought that at least a part of the claustrum had the same function as the amygdaloid nucleus. The physiological significance of this highly differentiated formation is obscure. Hilpert (1928) described the amygdala as being as complex in structure as the thalamus; Ariëns-Kappers et al (1936) regarded it as an olfacto-somatic correlation centre. It is pointless to discuss the unknown functions of the claustrum in terms of the unknown functions of the amygdala, but the amygdala appears to be connected to a suppressor mechanism.

In view of the resemblance between the claustrum of higher forms and the hyperstriatum of birds, Ariëns-Kappers (quoted by Berlucchi, 1927) suggested that the claustrum might have an indirect action on movement and orientation. The more recent work of Mettler and his colleagues (1939) has provided some evidence in favour of this hypothesis. These investigators found that exploration of the putamen and claustrum produced no observable effect on the behaviour of the animal studied (the Macaque was used). Electrical stimulation of claustrum and of putamen during the

course of cortically evoked movement, on the other hand, resulted in inhibition of such movement, persisting for a short time. Inhibition obtained from the claustrum appears to have been ipsilateral; bilateral inhibition was at times obtained from the putamen. Although the authors stated that spread of current to other structures could be excluded, the thinness of the claustrum medio-laterally, and the complexity of the adjacent capsules, suggest that spread of current to formations adjoining the claustrum could easily occur. The results obtained by stimulating the claustrum cannot therefore be conclusively attributed to the activation of claustral cells.

It is accordingly reasonable to assume that an inhibitor or "Suppressor" circuit is located in the region between claustrum and putamen. The relationship of the claustrum to such a circuit cannot be regarded as definitely established. (Stimulation of the claustrum by the strychnine-toluidine blue method would have given more exact information).

u | Suppressor circuits have been known for some years. According to recent summaries (Morin, 1948, Bucy, 1949, Fulton, 1949, Jefferson, 1950) they originate in certain cortical regions (of which that lying between areas 1 and 6 l.e. "1S" is best known) pass through the caudate nucleus, putamen, globus pallidus, and thalamus to reach the motor cortex. Although the links of this chain appear to have been demonstrated, the topography of the circuit (if it follows a circumscribed pathway) is undecided. Such a cir-

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cuit might well pass through, or be adjacent to, the external capsule, and would there be accessible to electrical stimulation.

Of the known components of the capsules, that described by Mettler, (1945) as "strio-external fibres" has some resemblance to the connections of the suppressor pathway. The fibres referred to by Mettler arose in the caudate nucleus, and passed ventrally through the medial parts of the external and extreme capsules; fibres from the putamen joined the system. Certain of the strio-external fibres, together with efferents from the globus pallidus, entered the homolateral stria terminalis; others continued into the anterior commissure. The strio-external fibres were present after removal of the cortex. The later course of these fibres differs from that usually ascribed to the suppressor circuits. The anterior commissure appears to be mainly an inter-temporal connection: it is not known to be connected with the thalamus or motor cortex. Mettler did not mention any connection between the claustrum and the strio-external system. The claustrum has, however, certain fibre connections similar to that system. It contributes fibres to the external capsule, and according to Winkler (quoted by d'Hollander, 1922) fibres derived from claustrum and striatum pass through the external capsule to the anterior commissure. The claustrum is also connected with the stria terminalis system (Kölliker, 1896); Berkelbach van der Sprenkel, 1926; Honegger, quoted by Probst, 1905). The anatomical evidence is suggestive, but proves neither that the strio-external system forms part of a sup-

pressor circuit, nor that the claustrum is connected with it.

In investigating the physiological significance of a structure such as the claustrum, it is usual to study the phenomena associated with its activation or destruction in an otherwise intact animal, and to attempt to correlate such phenomena with what is known about the synaptic relations of the cells of the structure. The syndromes of activation or destruction give a very distorted and partial view of the true function of the structure, if this be defined as its characteristic activity when unmodified and intact in an intact organism; indeed knowledge of function as so defined has scarcely yet been attained for any neural formation. In the case of the claustrum the matter is peculiarly difficult. The consequences of its damage or destruction are unknown. Stimulation of the claustral region produced inhibition of cortically evoked movement; this effect may have been caused by activation of neighbouring fibres. The formations to which the claustrum is known to be connected (lateral frontal cortex, especially area 9, orbital frontal cortex, prepiriform cortex, insular cortex and amygdaloid complex) are themselves of obscure physiological significance.

Stimulation of the insular cortex in conscious patients (Penfield and Rasmussen, 1950) produced abdominal sensation, possible secondary to increased gastro-intestinal motility. This is in agreement with v. Economo (1929), who suggested that insula and limbic

lobe represented the cortical station for autonomic and sympathetic systems. The orbital frontal cortex (areas 13 and 14) appears to be concerned with autonomic activities - respiration and temperature-control. Bilateral ablation of the orbital gyri in monkeys has produced profound restlessness; bilateral incision of the posterior part of area 14 produces "sham rage", (Fulton, 1949). These areas are known to have hypothalamic connections. The prefrontal cortex (area 9) is believed by Penfield and Rasmussen (1950) to be concerned with the elaboration of thought. Bilateral removal in monkeys was associated with mild spontaneous hyperactivity (Mettler, 1947b). It has hypothalamic connections, is reciprocally connected with medial and lateral thalamic nuclei (Mettler, 1947a) and has a well-developed connection with the caudate nucleus. It is not known to contain a suppressor strip. The relationship between the recently described secondary motor cortex and the claustrum is unknown. The temporal lobe may be concerned with "innemic" functions. These data are fragmentary and as yet unrelated. In ignorance it is wise to be silent; it may be conjectured that the claustrum represents a zone in which circuits concerned with autonomic function and skeletal muscle innervation mutually interact or "interfere", so that the neural correlates of emotional reverberations are enabled to enter into the elaboration of motor responses, while autonomic changes synergic to such responses are concurrently activated.

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CONCLUSIONS.

The claustrum, an irregular sheet of grey matter, is divisible (macroscopically) into dorsal (compact) and ventral (fragmented) portions. The dorsal part lies between insular cortex and putamen; it is separated from each by white matter (the extreme and external capsules) and is not exactly co-extensive with either grey formation. The lateral surface of the dorsal claustrum is irregular, the medial surface smooth. The irregularities of the lateral surface do not closely correspond to the undulations of the insular cortex; the medial surface approximately follows the curve of the putamen. The compact claustrum therefore varies in latero-medial width; it is usually broader in its lower part. The extreme capsule (between insular cortex and claustrum) and external capsule (between claustrum and putamen) vary in width throughout their extent. The extreme capsule does not fuse, at its limits, with the white matter of the hemisphere. ?
α α R
The ventral claustrum consists of a group of small grey masses adjacent to the inferior border of the dorsal claustrum. These masses (which vary in position and form from brain to brain) extend rostrally under the cortex of the superior surface of the temporal lobe, extending beyond the traditional limits of the insula. The most rostral "islands" constitute the "claustrum parvum" (of Landau). Elements of the ventral claustrum closely adjoin the temporal cortex and the lateral aspect of the amygdala. The fragmentation of the ventral claustrum is attributed to

the uncinata fasciculus and anterior commissure.

The dorsal claustrum is supplied by a group of branches of the middle cerebral artery which pierce the limen insulae.

Histologically the region between putamen and insular cortex constitutes a complex fibro-cellular reticulum. The fibres vary in diameter and pass in all directions; the cells (of various forms and sizes) are disposed without apparent order in the meshes of this reticulum. The central part of the reticulum contains a richer and more varied population of cells than the lateral or medial zones; its fibres, mainly of small diameter, form an intricate network. Fusiform, ovoid, triangular and polygonal cells are found in this region which corresponds to the macroscopic dorsal claustrum. The processes of these cells cannot be traced for any distance in the surrounding reticulum. The synaptic relationships between the claustral cells are unknown. The medial and lateral parts of the insular-putaminal zone correspond respectively to the external and extreme capsules. Their constituent fibres tend to be arranged in parallel strands; their cells are mainly ovoid and fusiform. These cells are dispersed and do not form "bridges" between claustrum and insular cortex or putamen. The fibres of each zone are intricately interlaced with those of the adjacent zone or zones. Fibres pass between putamen and external capsule. Compact bundles run across the superior part of the external capsule between putamen and claustrum. The radial bundles of the

insular cortex enter the extreme capsule; some pierce the claustral reticulum. The dorsal claustral zone appears to be relatively uniform histologically. The masses of the ventral claustrum closely resemble the dorsal claustrum in structure; they contain fewer fusiform cells. Dorsal and ventral claustrum are considered to form a histologically homogenous region. This claustral region is connected by "cell bridges" to the cortex of the olfactory trigone and to the basolateral amygdaloid nuclei. The claustral cells are known to have fibre-connections with the lateral and orbital frontal cortex, the pre-piriform cortex, insular cortex and possibly (through the stria terminalis) with certain olfactory nuclei and with the contralateral claustrum.

The capsular zones are known to contain intra-hemispherical (association) fibres, inter-hemispherical (commissural) fibres, auditory and somato-sensory radiations, olfactory and vestibular afferent fibres, striatal fibres and certain systems of unknown significance. Many of these fibres traverse the claustral zone.

Isolated lesions of the claustrum have neither been observed clinically nor produced experimentally. Damage to the insular-putaminal region is frequently, but not constantly, associated with speech disturbance. Electrical stimulation of the claustrum is said to produce (ipsilateral) inhibition of cortically evoked movement. The circuit responsible for this effect is unknown.

The claustrum has been thought to be concerned

with speech mechanisms and with the olfactory apparatus. There is no definite evidence in favour of these hypotheses.

The claustral cells are connected with lateral frontal and orbital cortex, prepiriform cortex and insular cortex. The claustrum is therefore connected to regions concerned with skeletal muscular activity and autonomic activity.

It is conjectured that in the claustral zone circuits concerned in skeletal muscular and autonomic function mutually interact or "interfere"; it is possible that this involves the integration of emotional correlates in motor responses, and in the activation of autonomic adjustments synergic to such responses.

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The mineral was analysed by Brown (1930). The mineral was treated with Citric Acid, impregnated with a dilute solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide.

In order to prepare the mineral for analysis, the mineral was ground to a fine powder, and the powder was then treated with a dilute solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide. The mineral was then ground to a fine powder, and the powder was then treated with a dilute solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide.

APPENDIX ON TECHNICAL METHODS.

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REFERENCES.

The mineral was analysed by Brown (1930). The mineral was treated with Citric Acid, impregnated with a dilute solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide. The mineral was then ground to a fine powder, and the powder was then treated with a dilute solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide.

MACROSCOPIC STAINING OF THE BRAIN.

The method used was that described by Brown (1939). The brain slices were treated with Carbolie Acid, impregnated with a mixed solution of Silver Nitrate and Lead Acetate, and reduced with Ammonium Sulphide.

In order to prepare the diagrams from these stained sections, a thin glass plate was superimposed on the section, and the outlines of the various structures drawn on the glass. The plate was then trans-illuminated, and the outlines drawn on tracing paper. The outlines for the final drawing were transferred from this by carbon paper.

A profile drawing of the hemisphere was made before sectioning in the macrotome. The reference line was added and the planes of section indicated by lines perpendicular to this reference line, spaced 5 m.m. apart. The vertical extent of the claustrum (in lateral view) was measured in each section and plotted on the corresponding vertical line, figure (1) being thus obtained.

HISTOLOGICAL STAINING METHODS.

The preliminary series of trial sections was stained by the following methods (the source of the technique used is indicated in each case): Borrell's Methylene Blue (Clayden, 1948), Bielschowsky's Silver Impregnation (Anderson, 1929), Krohnthal's Lead Sulphide Impregnation (Bolles-Lee, 1921) and Einarson's Gallocyanine Stain (Carleton, 1938).

The methods finally adopted, and used as a routine throughout the investigation, were Foley's Protargol-Gallocyanine Stain and Landau's Silver Impregnation.

The modification of Foley's original method (Foley, 1943) published by Gurr (1950) was used; the stain demonstrates nerve-fibres, Nissl-bodies, nuclei, and myelin sheaths, and thus gives a comprehensive picture.

The contrast obtained, although quite sufficient for visual microscopic examination, was sometimes inadequate for micro-photography.

The original technique for Landau's Silver Impregnation was followed (Landau, 1940). The method is rapid, and allows individual sections from ordinary paraffin blocks to be used. The process does not appear to be well known in this country (it is not included in the usual reference books), and will therefore be summarized below.

1. Paraffin sections of formol-fixed material are brought down to distilled water.
2. Section placed in 4% formol for 12 - 24 hours.
3. Rapid wash with distilled water.
4. Section placed in a Petri dish and covered with 20% aqueous solution of Silver Nitrate. This solution is allowed to act for 1 - 2 hours. The closed Petri dish should be kept in an oven at 35°C.
5. Rapid wash with distilled water.
6. Cover section with 20% Ammoniacal Silver Nitrate, and allow to act for 3 minutes.

7. Rapid wash with distilled water.
8. Add a few drops of 1% Formol to reduce the silver. (The result should be examined under the microscope; steps 6, 7 and 8 may be repeated if impregnation is inadequate. If the section is too deeply impregnated, it should be washed with 1% Acetic Acid or 10 - 15% Potassium Iodide solution).
9. Dehydrate in alcohols, clear in Xylol and mount in Canada Balsam.

It is advisable to filter the Silver Nitrate and Ammoniacal Silver Nitrate solution immediately before applying them to the sections.

Landau's Ammoniacal Silver Nitrate solution is prepared by taking a few m.l. of 20% aqueous solution of Silver Nitrate in a dropping-bottle and adding 20% Ammonia solution to it, drop by drop, until the turbidity first produced has just disappeared and the resulting solution has become perfectly clear. The method gives a general view of cell-body and processes, compared by Landau to that obtained by Cajal's procedure. The fibres are more readily impregnated^g than the cell-body. Slight excess of ammonia in the ammoniacal silver accentuates the impregnation. (The micro-photographs were prepared by the Photographic Unit, Royal Society of Medicine.)

TECHNICAL REFERENCES.

Anderson: J. (1929) "How to Stain the Nervous System"
Edinburgh: E. & S. Livingstone.

- 611 -

Bolles-Lee: A. (1921) "Microtomists Vade-mecum" 8th
Edition (Edited Bronté-Gatenby) London: J. & A.
Churchill.

Brown: D.B. (1939) Anat. Rec. 79. 419.

Carleton: H.M. (1938) "Histological Technique" 2nd Ed.
Oxford: University Press.

Clayden: E.C. (1948) "Practical Section - Cutting and
Staining" London: J. & A. Churchill.

Foley: J.O. (1943) Stain Techn. 18. 27.

Gurr: E. (1950) "Microscopic Staining Techniques: No. 2".
London: E. Gurr.

Landau: E. (1940) Schweiz. med. Wschr. 70. 1273.

REFERENCES.

- Ariëns-Kappers: C.U., Huber: G.C. Crosby: E. (1936).
"Comparative Anatomy of the Nervous System of
Vertebrates, including Man", 2v. New York:
Macmillan.
- Ayala: G. (1915). "A hitherto undifferentiated nucleus
in the fore-brain (nucleus subputaminalis)"
Brain. 38. 433.
- (1924) "Weitere Untersuchungen über den Nucleus
subputaminalis", J. Psychol. Neurol., Lpz. 30.
285.
- Bechterew: W. v. (1899) "Die Leitungsbahnen im Gehirn
und Rückenmark", 2nd Ed., Leipzig: A. Georgi.
- Beevor: C.E. (1909). Philos. Trans. 200. (Ser.B.) 1.
Quoted by Shellshear (1920).
- Berkelbach van der Sprenkel: H. (1926). "Stria termin-
alis and Amygdala in the brain of the Opossum",
J.Comp. Neurol. 42. 211.
- Berlucchi: C. (1927). "Ricerche di Fine anatomia sul
claustrum e sull' insula del gato". Riv.
sper. Freniat. 51. 125.
- Bianchi: L. (1922) "The Mechanism of the Brain and the
Function of the Frontal Lobes". (Transl. J.H.
Macdonald) Edinburgh: E. & S. Livingstone.
- Böhne: C. (1926) "Über die arterielle versorgung des
Gehirns: 1. Über die arterielle Blutversorgung
der subcorticalen Ganglien" ges. Anat. 81.
151.
- Bonin: G. v. (1950) "Essay on the Cerebral Cortex",
Springfield: C. Thomas.
- Brockhaus: H. (1938) "Zur normalen und pathologischen
Anatomie des Mandelkerngebietes", J. Psychol.
Neurol. Lpz. 49. 1.
- (1940) J. Psychol. Neurol. Lpz. 49. 249. (not
available)
- Brodal: A. (1947) "The Hippocampus and the sense of
Smell". Brain. 70. 179.
- Brodmann: K. (1909). "Vergleichende Lokalisationslehre
der Grosshirnrinde", Leipzig: J.A. Barth.
- Bruce: A. (1890) "On the absence of the corpus callosum
in the human brain, with the description of a
new case", Brain. 12. 171.
- Bucy: P.E. (Editor). (1949) "The precentral motor
cortex". Urbana: University of Illinois Press.

- Cajal: S. Ramon y. (1902) "Studien über Hirnrinde des Menschen", (1900-1906), (Transl. J. Bresler) Leipzig: J.A. Barth. (Heft. 3. 1902).
- (1911) "Histologie du système nerveux de l'homme et des vertébrés". 2v. 1909, 1911. Paris: A. Maloine.
- Campbell: A.W. (1905) "Histological studies on the localization of Cerebral Function", Cambridge: University Press.
- Crouch: R.L., Thompson: J.K., (1938). "The efferent fibres of the thalamus of *Macacus rhesus*: 1. Lateral and ventral nuclei", J. comp. Neurol. 69. 255.
- Déjerine: J. (1895). "Anatomie des centres nerveux" 2 v. 1895, 1901. Paris: Rueff et cie
- Duret: (1873, 1874) Arch. Physiol. Quoted by Shellshear (1920)
- Economo: C.v. (1929) "The Cytoarchitectonics of the Human Cerebral Cortex", Oxford: University Press.
- Foix: C., Nicolesco: J. (1925). "Les noyaux gris centraux et la région mésencéphalo-sous-optique". Paris: Masson et cie.
- Fox: C.A., Rambach: W., (1945). "A Marchi study of the distribution of the anterior commissure in the monkey". Anat. Rec. 91. 274.
- Fisher: R.R., Desalva: S.J. (1948) "The distribution of the anterior commissure in the monkey", (*Macaca mulatta*). J. comp. Neurol. 89. 245.
- Fulton: J.F. (1949). "Functional Localization in the Frontal Lobes and Cerebellum". Oxford: Clarendon Press.
- Hilpert: P. (1928) "Der Mandelkern des Menschen", J. Psychol. Neurol: Lpz. 36. 44.
- Holl: M. (1902) "Über die Insel des Menschen- und Anthropoiden Gehirns". Arch. Anat. Physiol: Lpz. 1.
- ✓ Hollander: F. (1922) "Contribution à l'étude anatomo - expérimentale de la capsule externe et de la commissure antérieure", Bull. Acad. Méd. Belg. 5 ième Sér. 2. 211.
- Hösel: K. (1905). "Über die Markreifung der Sogenannten Körperfühls-sphäre und der Riech - und Sehstrahlung des Menschen". Archiv. Psychiat. Nervenkr. 39. 195.

Itabasi: K. (1928) "Pri la arterioj de la bazaj kernoj de cerbo". Folia. anat. Japon. 6. 617.

Jefferson: Sir G. (1950) "Localization of function in the cerebral cortex". Brit. med. Bull. 6. 333.

Jelgersma: G. "Atlas Anatomicum Cerebri Humani", plates reproduced in Ranson's "Anatomy of the Nervous System" 8th Ed. (Ed. Clark) 1947 Philadelphia: W.B. Saunders Company.

Kodama: S. (1927) "Über die sogenannten Basalganglionen: II Pathologisch-anatomische Untersuchungen mit Bezug auf die sogenannten Basalganglionen und ihre Adnexe". Schweiz. Arch. Neurol. Psychiat., 20. 209.

Kölliker: A. (1896) "Handbuch der Gewebelehre des Menschen" (Band 2) Leipzig: W. Engelmann.

Környey: S. (1926) "Zur Faseranatomie des Striatum, des Zwischen und Mittelhirns auf Grund der Markreifung in der ersten drei Lebensmonaten". Z. ges. Anat. 81. 620.

Krieg: W.J.S. (1947) "Connections of the cerebral cortex: 1. The albino rat. c. Extrinsic Connections" J. comp. Neurol., 86. 267.

Kuhlenbeck: H. (1924) "Über den Ursprung des Basalganglien des Grosshirns", Anat. Anz. 58. 49.

Laere: J. van (1943) (Study of central vestibular pathways) Mém. Acad. Roy. Méd. Belgique 2 ième. Sér. Vol. 2. Fasc. 1.

Landau: E. (1918). "Die Vorderhirnganglien". Schweiz. Arch. Neurol. Psychiat. 3. 95.

----- (1919) "The Comparative anatomy of the nucleus amygdalae, the claustrum and the insular cortex". J. Anat. Lond. 53. 351.

----- (1923) "Zur Kenntnis der Beziehung des Claustrums zum Nucleus Amygdalae und zur Area piriformis, im speziellen zum Tractus olfactorius", Schweiz. Arch. Neurol. Psychiat., 13. 391.

----- (1936) "Quelques nouvelles considérations sur l'avant mur". Arch. Anat. Strasbourg. 23. p.165.

----- (1937) "Un nouveau champ de substance grise dans le cerveau humain". Bull. Soc. vaud. Sci. Nat. 59. No.244.

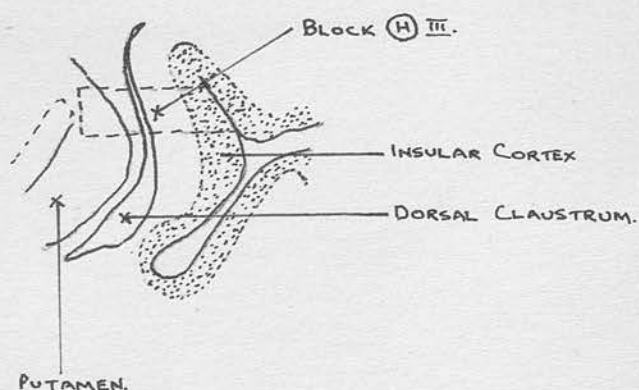
----- (1938) "Le claustrum parvum chez l'Homme". Mém. Soc. vaud. Sci. nat. 6. No.2 (No.41).

- Landau: E. (1939) "La Myéloarchitectonique insulaire et l'Avant-mur". Schweiz. Arch. Neurol. Psychiat., 43. 287.
- Lange: C. de (1925). "On brains with total and partial lack of the corpus callosum and on the nature of the longitudinal callosal bundles". J. nerv. ment. dis. 62. 449.
- Lauer: E.W. (1945) "The nuclear pattern and fibre connections of certain basal telencephalic centres in the Macaque". J. comp. Neurol. 82. 215.
- Lockard: I. (1948) "Certain developmental relations and fibre connections of the triangular gyrus in primates". J. comp. Neurol. 89. p.349.
- Macchi: G. (1947) "Il problema del Claustro umano del punto di vista ontogenetico". Commentationes Pontifica Academia Scientiarum. 11. 205.
- (1948) "Sulla morfologia, struttura e rapporti del Claustro nell 'Uomo". Cervello. 24. 1.
- Manoia: A.R. (1912). "Contributo clinico ed anatomo-patologico alla studio delle lesione subinsulari de sinistra". Riv. Patol. nerv. ment. 17. 129.
- Marburg: O. (1927). "Mikroskopisch-topographischer Atlas der Menschlichen Zentralnerven systems". 3d. Ed. (Text). Leipzig: F.Deuticke.
- Mettler: F.A. (1935a). "Corticifugal fibre connections of the cortex of Macaca mulatta. The frontal region". J. comp. Neurol. 61. p.509.
- (1935b). "Corticifugal fibre connections of the cortex of Macaca mulatta. The parietal region". J. comp. Neurol. 62. p.263.
- , Ades: H.W., Lipman: E., Culler: E.A., (1939). "The extra-pyramidal system. An experimental demonstration of function". Arch. Neurol. Psychiat. Chicago., 41. 984.
- (1945). "Fibre connections of the corpus striatum of the monkey and baboon", J. comp. Neurol. 82. 169.
- (1947a) "Extra-cortical connections of the primate frontal cerebral cortex. I. Thalamo-cortical connections". J. comp. Neurol. 86. 95.
- (1947b). "Extra-cortical connections of the primate frontal cerebral cortex. II. Corticifugal connections". J. comp. Neurol. 86. 119.

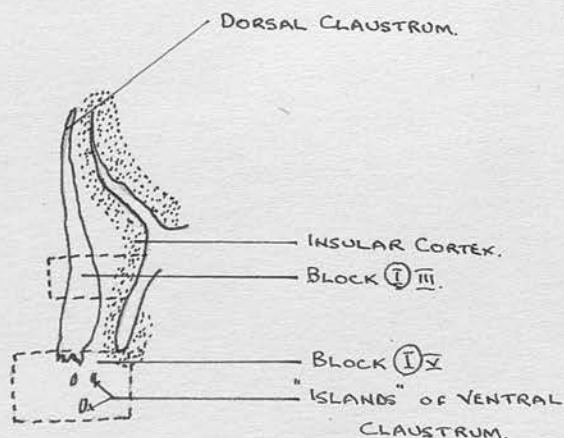
- Meyer: M., Allison: A.C., (1949) "An experimental investigation of the connections of the olfactory tracts in the monkey". J. Neurol., Neurosurg., Psychiat. 12. 274.
- Mingazzini: G. (1901) "Sulla sintomatologia delle lesioni del nucleo lenticolare". Riv. sper. Freniat. 27. 68.
- Mondino: C. (1885). "Untersuchungen über die Vormauer und über Mandelkern". Int. Mschr. Anat. Physiol. 2. 245.
- Morin: G. (1948). "Physiologie du Système Nerveux Central". Paris: Masson et Cie.
- Muskens: L.J.J. (1922). "The central connections of the vestibular nuclei with the corpus striatum, and their significance for ocular movements and locomotion". Brain. 45. 454.
- Nielsen: J.M. (1946). "Agnosia, Apraxia, Aphasia: their value in cerebral localization". 2nd. Ed. New York: P.B. Hoeber.
- Niemer: W.T., Papez: J.W. (1945). "Nuclear masses of amygdala of chimpanzee from graphic reconstructions". Anat. Rec. 91. 291.
- Papez: J.W. (1938). "Reciprocal connections of the striatum and pallidum in the brain of Pithecus (Macacus) Rhesus". J. comp. Neurol. 69. 329.
- (1945). "Fibre tracts of the amygdaloid region in the human brain from a graphic reconstruction of the fibre connections and nuclear masses". Anat. Rec. 91. 294.
- Peele: T.L. (1942). "Cytoarchitecture of individual parietal areas in the monkey (Macaca mulatta) and the distribution of the efferent fibres". J. comp. Neurol. 77. 693.
- Penfield: W., Rasmussen: T., (1950). "The Cerebral Cortex of Man". New York: The Macmillan Co.
- Pintus: G.S. (1930) "Struttura cellulare e citoarchitettura dell' antimuro umano". Riv. Neurol. 3. 289.
- (1931) "Forma e connessioni grigie dell' antimuro umano". Arch. gen. Neurol. Psychiat. 12. 16.
- (1932). "Connessioni bianche dell' antimuro umano". Arch. gen. Neurol. Psychiat. 13. 9.
- Poliak: S. (1932). "The Main Afferent Fibre Systems of the Cerebral Cortex in Primates". (University of California Publications in Anatomy: Vol.2). Berkeley: University of California Press

- Probst: M. (1905). "Weitere Untersuchungen über die Grosshirnfaserung und über Rindenreizversuche nach Ausschaltung verschiedener Leitungsbahnen" S.B. Akad. Wiss. Wien. 114. 173.
- Randacio: F. (1882). "On the relations of the Nucleus taeniformis with the olfactory nerve". J. Anat. Lond. 16. 151.
- Rose: M. (1928). "Die Inselrinde des Menschen und der Tiere". J. Psychol. Neurol. Lpz. 37. 467.
- Rundles: R.W., Papez: J.W. (1938) "Fibre and cellular degeneration following temporal lobectomy in the monkey". J. comp. Neurol. 68. 267.
- Shellshear: J.L. (1920). "The basal arteries of the forebrain and their functional significance". J. Anat. Lond. 55. 27.
- Smith: Sir G. Elliot (1919). "A preliminary note on the morphology of the corpus striatum and the origin of the neopallium". J. Anat. Lond. 53. 271.
- Spatz: H. (1922). "Über den Eisennachweis in Gehirn, besonders in Zentren des extrapyramidal-motorischen Systems". Z. ges. Neurol. Psychiat. 77. 261.
- Spiegel: E. (1919). "Die Kerne im Vorderhirn der Säuger". Arb. Neurol. Inst. Univ. Wien. 22. 418.
- Stoecker: W. (1912). "Über Balkenmangel im Menschlichen Gehirns". Arch. Psychiat. Nervenkr. 50. 543.
- Völsch: M. (1906). "Zur vergleichenden Anatomie des Mandelkerns und seiner Nachbargebilde". Arch. mikr. Anat., 68. 573.
- (1911). "Zur vergleichenden Anatomie des Mandelkerns und seiner Nachbargebilde II" Arch. mikr. Anat., 76. 373.
- Weigert: (1910). "Encyclopädie der Mikroskop. Technik. vol. 2. (2nd ed.) p.234. (quoted by Landau (1939), above.)
- Wernicke: (1881) "Lehrbuch der Gehirnkrankheiten". 2v. (Vol.1.)
- Whitaker: J.R. (1921). "Anatomy of the Brain and Spinal Cord" 5th Ed. Edinburgh: E.S. Livingstone.
- Wilson: S.A.K. (1914) "An experimental research into the anatomy and physiology of the corpus striatum". Brain. 36. 427.

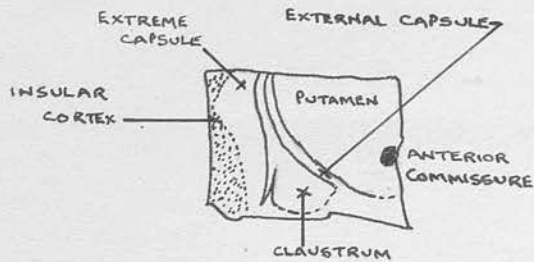
APPENDIX 2: DIAGRAMS SHOWING LOCATION OF BLOCKS
FROM WHICH MICRO-PHOTOGRAPHS WERE PREPARED.



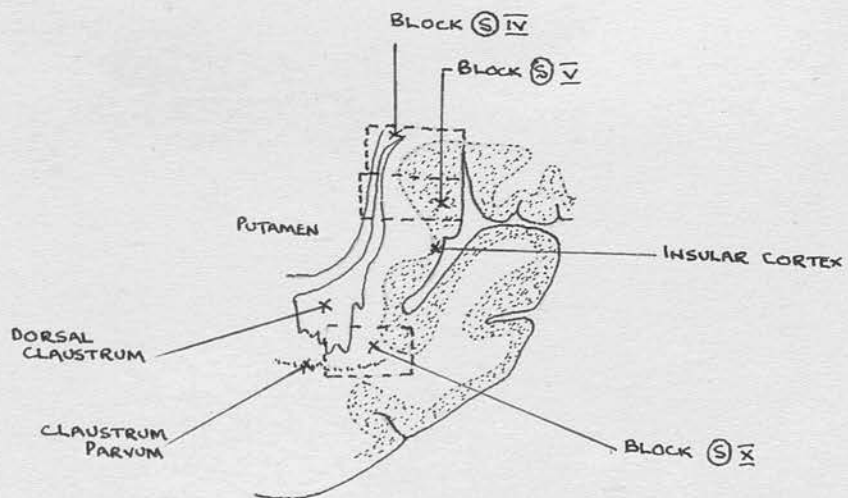
LOCATION OF BLOCK (H) III. MACROTOME AND
MICROSCOPIC SECTIONS IN FRONTAL-VERTICAL PLANE.



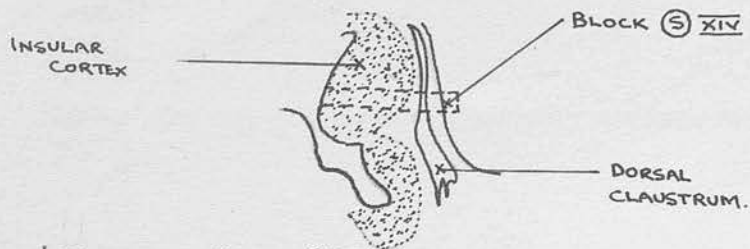
LOCATION OF BLOCKS (I) III AND (I) V. MACROTOME
AND MICROSCOPIC SECTIONS IN FRONTAL-VERTICAL PLANE.



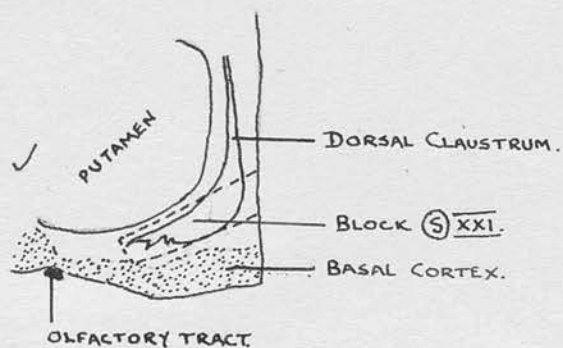
TOPOGRAPHIC FEATURES OF BLOCK (S) I. MACROTOME AND MICROSCOPIC SECTIONS IN FRONTAL-VERTICAL PLANE.



LOCATION OF BLOCKS (S) IV, (S) V, AND (S) X. MACROTOME AND MICROSCOPIC SECTIONS IN FRONTAL-VERTICAL PLANE.



LOCATION OF BLOCK (S) XIV. MACROTOME SECTION IN
FRONTAL-VERTICAL PLANE, MICROSCOPIC SECTIONS
CUT IN HORIZONTAL PLANE



LOCATION OF BLOCK (S) XXI. MACROTOME SECTION IN
FRONTAL-VERTICAL PLANE, MICROSCOPIC SECTIONS
CUT IN OBLIQUE PLANE (PARALLEL TO SUPERIOR
SURFACE OF BLOCK).